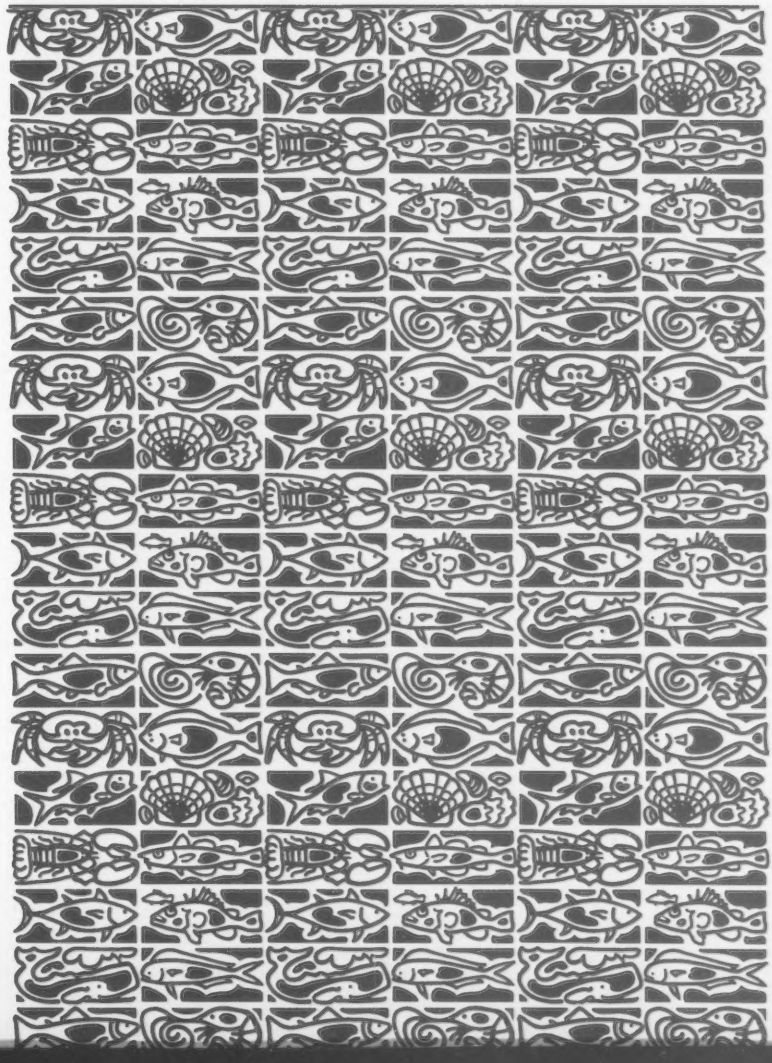
U.S. Department
of Commerce

Volume 90
Number 4
October 1992

Fishery Bulletin



U.S. Department of Commerce
Barbara Hackman Franklin
Secretary

National Oceanic and Atmospheric Administration
John A. Knauss
Under Secretary for
Oceans and Atmosphere

National Marine Fisheries Service
William W. Fox Jr.
Assistant Administrator
for Fisheries

The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Second class postage is paid in Seattle, Wash., and additional offices. POSTMASTER send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, Attn: Chief, Mail List Branch, Mail Stop SSOM, Washington, DC 20402-9373.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $24.00 domestic and $30.00 foreign. Cost per single issue: $12.00 domestic and $15.00 foreign. **See back page for order form.**

Fishery Bulletin

Scientific Editor
Dr. Linda L. Jones
Northwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, Washington 98112-2097

Editorial Committee
Dr. Andrew E. Dizon National Marine Fisheries Service
Dr. Charles W. Fowler National Marine Fisheries Service
Dr. Richard D. Methot National Marine Fisheries Service
Dr. Theodore W. Pietsch University of Washington
Dr. Joseph E. Powers National Marine Fisheries Service
Dr. Tim D. Smith National Marine Fisheries Service
Dr. Mia J. Tegner Scripps Institution of Oceanography

Managing Editor
Nancy Peacock
National Marine Fisheries Service
Scientific Publications Office
7600 Sand Point Way NE, BIN C15700
Seattle, Washington 98115-0070

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

U.S. Department
of Commerce
Seattle, Washington

Volume 90
Number 4
October 1992

Fishery Bulletin

Contents

633 **Allen, Larry G., and Michael P. Franklin**
Abundance, distribution, and settlement of young-of-the-year white seabass *Atractoscion nobilis*, in the Southern California Bight, 1988-89

642 **Boggs, Christofer H.**
Depth, capture time, and hooked longevity of longline-caught pelagic fish: Timing bites of fish with chips

659 **Boothroyd, Frank A., and Gerald P. Ennis**
Reproduction in American lobsters *Homarus americanus* transplanted northward to St. Michael's Bay, Labrador

668 **Ditty, James G., and Richard F. Shaw**
Larval development, distribution, and ecology of cobia *Rachycentron canadum* (Family: Rachycentridae) in the northern Gulf of Mexico

678 **Edwards, Elizabeth F.**
Energetics of associated tunas and dolphins in the eastern tropical Pacific Ocean: A basis for the bond

691 **Eggleston, David B., Romuald N. Lipcius, and David L. Miller**
Artificial shelters and survival of juvenile Caribbean spiny lobster *Panulirus argus*: Spatial, habitat, and lobster size effects

703 **Graves, John E., Jan R. McDowell, Ana M. Beardsley, and Daniel R. Scoles**
Stock structure of the bluefish *Pomatomus saltatrix* along the mid-Atlantic coast

711 **Leffler, Deborah L., and Richard F. Shaw**
Age validation, growth, and mortality of larval Atlantic bumper (Carangidae: *Chloroscombrus chrysurus*) in the northern Gulf of Mexico

720 **Parrish, Frank A., and Thomas K. Kazama**
Evaluation of ghost fishing in the Hawaiian lobster fishery

726 **Pearcy, William G.**
Movements of acoustically-tagged yellowtail rockfish *Sebastes flavidus* on Heceta Bank, Oregon

736 **Restrepo, Victor R., John M. Hoenig, Joseph E. Powers, James W. Baird, and Stephen C. Turner**
A simple simulation approach to risk and cost analysis, with applications to swordfish and cod fisheries

749 **Schilling, Mark R., Irene Seipt, Mason T. Weinrich, Steven E. Frohock, Anne E. Kuhlberg, and Phillip J. Clapham**
Behavior of individually-identified sei whales *Balaenoptera borealis* during an episodic influx into the southern Gulf of Maine in 1986

756 **Somerton, David A., and Bert S. Kikkawa**
Population dynamics of pelagic armorhead *Pseudopentaceros wheeleri* on Southeast Hancock Seamount

770 **Utter, Fred M., Robin S. Waples, and David J. Teel**
Genetic isolation of previously indistinguishable chinook salmon populations of the Snake and Klamath rivers: Limitations of negative data

Notes

778 **Jensen, Gregory C., Helle B. Andersen, and David A. Armstrong**
Differentiating *Paralithodes* larvae using telson spines: A tail of two species

784 **Matthews, Kathleen R.**
A telemetric study of the home ranges and homing routes of lingcod *Ophiodon elongatus* on shallow rocky reefs off Vancouver Island, British Columbia

791 **Miller, George W.**
An investigation of dolphin *Tursiops truncatus* deaths in East Matagorda Bay, Texas, January 1990

798 **Secor, David H.**
Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Morone saxatilis*

807 **Skillman, Robert A., and George H. Balazs**
Leatherback turtle captured by ingestion of squid bait on swordfish longline

809 **Taylor, Ronald G., and Michael D. Murphy**
Reproductive biology of the swordfish *Xiphias gladius* in the Straits of Florida and adjacent waters

817 **Index, Volume 90**

Abundance, distribution, and settlement of young-of-the-year white seabass *Atractoscion nobilis* in the Southern California Bight, 1988-89*

Larry G. Allen

Department of Biology, California State University, Northridge, California 91330

Michael P. Franklin

Department of Biology, California State University, Northridge, California 91330
Present address: Department of Biological Sciences
University of California, Santa Barbara, California 93106

Abstract. – Commercial and sport landings of white seabass have declined, particularly in southern California, and the populations now appear to be severely impacted. To provide information critical to the management of this species, settlement patterns of white seabass within the Southern California Bight were investigated for 1988–89. Data were obtained from 16 stations sampled along the southern California coastline during June–October 1988, and at 12 stations sampled along the coasts of the mainland and four Channel Islands May–August 1989. At each station, four 5-minute tows were taken with a 1.6 m beam trawl at each of two depths, 5 and 10 m.

Most young-of-the-year white seabass were <10 mm SL and had settled within 2–3 weeks of capture. Density estimates for white seabass off southern California were low, ranging from 0.3 to only 37.8 individuals per hectare. In 1988, catch-per-unit-effort (CPUE) peaked in July (1.10/tow) with differences being statistically significant among months. In 1989, CPUE peaked in June (0.45/tow) with differences being statistically significant among distance blocks from the mainland. CPUE was 15 times higher at the mainland stations compared with the island stations (0.59/tow vs. 0.04/tow). Abundance was significantly correlated with warm bottom-water temperatures in 1988, although not in 1989.

Multivariate analysis of the catches with selected environmental variables indicated that distance from the mainland and bottom temperature may have been important factors influencing settlement. However, in combination, these two variables accounted for only 5% of the total variance (R^2 0.05) in abundance. This finding implies that other factors, most notably the availability of premetamorphic larvae, probably have an influence on white seabass settlement and need to be considered in future studies.

Manuscript accepted 8 July 1992.
Fishery Bulletin, U.S. 90:633–641 (1992).

The white seabass *Atractoscion nobilis* is the largest croaker (family Sciaenidae) occurring off southern California (Miller and Lea 1974), where it is important in both commercial and sport fisheries. Despite attempts to improve the fishery (e.g., imposing minimum size requirements and limits on sport and commercial catches; Frey 1971), landings continue to decline and the stocks appear to be severely impacted (Vojkovich and Reed 1983), particularly in southern California waters.

Despite their impacted status and economic importance, little was known about the early-life-history stages of white seabass until recently. Moser et al. (1983) described the larval development from hatchery-reared eggs. Field investigations of early-life-history stages were limited to reports of larval occurrence within California Cooperative Fisheries Investigations (CalCOFI) collections from 1950 to 1978. For example, Moser et al. (1983) found that only 15% of white seabass larvae were taken in southern California waters. Most were taken near Sebastian Viscano and San Juanico Bays, Baja California.

A few studies have provided limited information on the young-of-year (YOY) stages of white seabass. Allen and Franklin (1988) examined the abundance and distribution of juvenile white seabass in the vicinity of Long Beach harbor and developed a model for locating YOY white seabass in coastal waters. We observed that YOY white seabass were captured over sandy bottoms in shallow water near the breaker line, most often with submerged aquatic vegetation (drift algae: green, brown, and red), encrusting bryozoans, and terrestrial debris. This area seems to be the nursery grounds for white seabass. The drift material may be an important component of these nursery areas because these fish appear to be structure-oriented early in life (Allen and Franklin 1988, Margulies 1989, Donohoe 1990). Donohoe (1990), based on field collections, found that young seabass were associated with the drift, and also observed that the larvae and juveniles moved toward structures in laboratory experiments. A significant relationship was found between the mass of drift algae and the occurrence of YOY white seabass from Oceanside, California to the Mexican border, suggesting that the drift habitat may influence the distribution patterns

* Contribution 67 of the Ocean Studies Institute, California State University.

of these young fish (Donohoe 1990). Margulies (1989) concluded that the visual perception of YOY seabass improves with age, and that young fish begin to avoid predators by moving to the drift.

Our studies on white seabass settlement were undertaken in southern California where the main fishery for this species still exists. The specific objectives were to (1) examine the patterns of abundance, distribution, and settlement of YOY white seabass off the coast of southern California between Point Conception and San Mateo Point and along the coastlines of four of the larger Channel Islands, and (2) identify environmental factors that may influence these patterns.

Materials and methods

YOY white seabass were captured during the summers of 1988 and 1989 as part of the Ocean Resources Enhancement and Hatchery Program (OREHP) of the California Department of Fish and Game, which emphasized studies within the Southern California Bight. Trawls were made over flat bottoms just offshore of open sand beaches, using two 5.2 m whalers. At each station four 5-minute replicate tows were made in the shallow, potential nursery areas by two whalers simultaneously sampling along each of two isobaths (5 and 10 m) using a 1.6 m beam trawl. The trawl was comprised of 4 mm mesh in the wings and 2 mm knotless mesh in the codend. Calibration tows using a meter wheel indicated that a 5-minute tow covered an average of 183 m of bottom, yielding a mean coverage of 293 m^2. Bottom profiles were monitored using depth finders mounted in each whaler. Temperature, salinity, dissolved oxygen, and pH were monitored at the surface and bottom at each station at both isobaths, using a Hydrolab Surveyor II Water Quality Measurement System. Submerged aquatic vegetation (drift algae) captured in each tow was weighed (to nearest kg) at all stations. White seabass were measured to the nearest 0.1 mm standard length (SL).

Sixteen stations were established along the coast of southern California from Point Conception to San Mateo Point in 1988 (Fig. 1). These stations were approximately 10 nmi apart and were sampled from June through October. The sampling regime yielded 128 tow samples (4 tows at 2 depths at each of 16 stations) over 5 months, for a total of 640 tow samples in 1988.

In 1989, sampling was designed to examine the settlement patterns along the mainland and around the four largest offshore islands. Four mainland stations and eight island stations were sampled each month from May through August (Fig. 1). The mainland stations were those with the greatest consistency of catch of YOY white seabass in 1988: Stns. 6 (Ventura), 10 (Malibu), 13 (Belmont Shore), and 15 (Laguna Beach). Two new stations were established at each of four Channel Islands: Stns. 17 and 18 (Santa Cruz), 19 and 20 (Santa Rosa), 21 and 22 (Santa Catalina), and 23 and 24 (San Clemente). The twelve stations sampled in 1989 were divided subjectively into three groups of four stations based on relative distance from shore or distance blocks (DSTBLK). Stns. 6, 10, 13, and 15 were designated as being at the mainland (MAINLAND); Stns. 17, 18, 21, and 22 as near-island stations (NEAR ISL); and Stns. 19, 20, 23, and 24 as far-island stations (FAR ISL). The 1989 sampling regime yielded 96 tow samples (4 tows at 2 depths at each of 12 stations) for each month except May, when only 80 tows were made because poor weather conditions prevented sampling the Santa Rosa Island stations, for a total of 368 tows overall.

Analysis of variance, t-test, and correlation analyses were completed using the CSS:Statistica for desktop computers (Stat Soft, Inc., Tulsa). For 1988 data, a

Figure 1
Map of locations of mainland and Channel Island stations sampled during the YOY white seabass *A. nobilis* survey, 1988–89.

balanced design, three-way ANOVA was used to test the effects on catch-per-unit-effort (CPUE) of combinations of independent variables (station, month, and depth). In 1989, a similar three-way ANOVA design was used to test the effects of distance block (distance from the mainland), month, and depth on CPUE. CPUE was used in all parametric analyses in order to minimize any negative impact that the large number of zero-catch tows would have on the analysis. Since replicates had to be combined, the three-way-interaction mean square was utilized as a conservative estimate of sampling error for the 1988 ANOVA test. In 1989, the ANOVA design was unbalanced due to two missing stations in May at Santa Rosa Island. In this case, cell means estimation was utilized to overcome the imbalance. Since the three-way-interaction term was originally found to be significant in the 1989 analysis, its mean square was pooled with the within-sample error in order to partition out the effect of the interaction on the main effects of distance block, month, and depth individually. Correlations and canonical correlation analysis were utilized to examine the possible association of various environmental factors with settlement of YOY white seabass.

Results

Length-frequencies

The YOY white seabass captured during the 1988 survey ranged from 4.2 to 78 mm SL ($\bar{x}$ 9.8 mm SL). In 1989, the range was 4.5–51.7 mm SL ($\bar{x}$ 12.1 mm SL). Most YOY, however, ranged from 5 to 20 mm SL (Fig. 2). Newly settled fish (<10 mm SL) were caught from June through September. Individuals >20 mm SL were more common from July through October.

Newly settled fish (<10 mm SL) made up 75% of all YOY seabass in 1988 and 1989. Fish <20 mm SL comprised 93% of the total catch. The paucity of larger YOY in the samples (Fig. 2) from July to September indicates that our beam-trawl catch may be biased toward smaller, less-mobile fish.

Studies utilizing the daily growth rings on white seabass otoliths (Franklin and Allen, unpubl. data) indicate that fish of 5–20 mm SL are ~37–104 days old. Since settlement occurred consistently at ~5 mm SL, white seabass in this range settled at 0–68 days before capture. The majority of those <10 mm SL had settled 14–21 days before capture.

Abundance and distribution

Summer 1988 Sampling along the mainland yielded 270 YOY white seabass. Most (58%) were captured at five of the 16 stations: Stn. 2 (Refugio Beach, *n* 38), Stn. 6 (Ventura, *n* 28), Stn. 10 (Malibu, *n* 30), Stn. 13 (Belmont Shore, *n* 31), and Stn 15 (Laguna Beach, *n* 31) (Fig. 3). Mean catches (CPUE) were highest at these five stations; furthermore, the variance of these five means was also very high. This was especially true at Stn. 2 (Refugio Beach) where 36 of the 38 YOY captured were taken during a single month (July).

The CPUE for all stations was low in June 1988 (0.15 individuals/tow), peaked in July (1.10/tow), and declined to 0.08/tow in October (Fig. 4). Catches in July accounted for 52% (141 individuals) of YOY white seabass taken in 1988. In June, catch was low (19 individuals) and white seabass were collected only from southern stations (12, 13, and 15) (Fig. 5). By July,

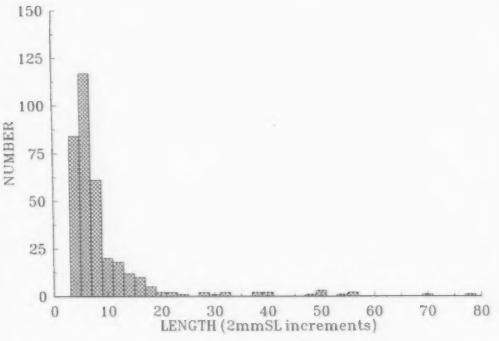


Figure 2
Length-frequencies of YOY white seabass *A. nobilis* from all samples combined, 1988–89. Length increments are 2 mm (*n* 354).

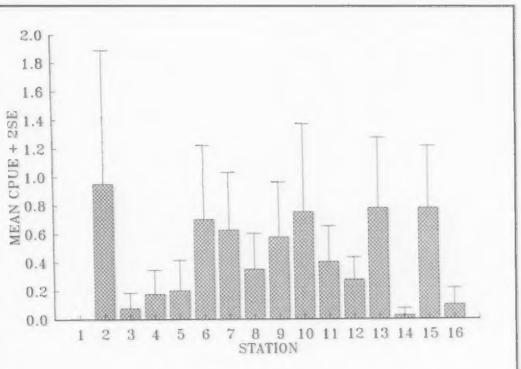


Figure 3
CPUE of YOY white seabass *A. nobilis* by station, summer 1988. Bars represent 2 SE of the mean.

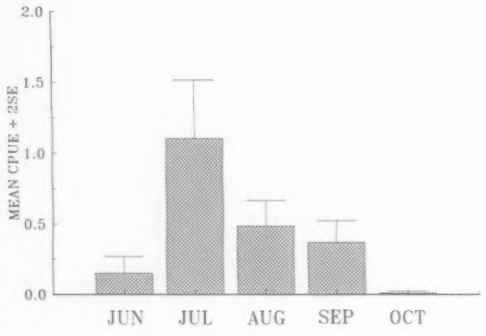


Figure 4
CPUE of YOY white seabass *A. nobilis* by month, summer 1988. Bars represent 2SE of the mean.

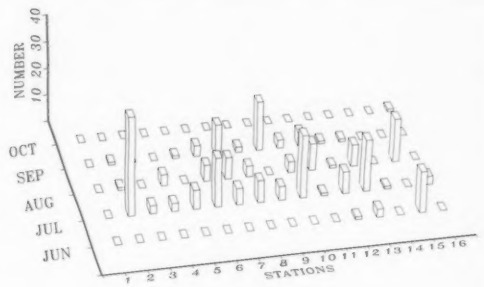


Figure 5
Abundance of YOY white seabass *A. nobilis* by station over the five months (June–October) of the 1988 survey.

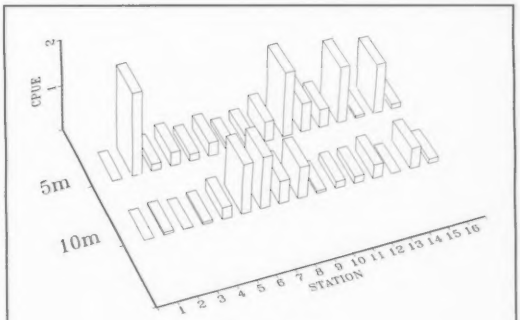


Figure 6
CPUE of YOY white seabass *A. nobilis* by station and depth for the 1988 survey.

relatively heavy settlement was observed throughout the coastal area, as far north as Stn. 2. The greatest numbers were taken off Stns. 2 (Refugio Beach), 6 (Ventura), 10 (Malibu), and 13 (Belmont Shore). None were taken at Stn. 15 (Laguna Beach) where they were most abundant a month earlier. In August, the number of recently-settled white seabass had declined from the July peak. Moderate numbers were captured at Stns. 7 (Hueneme), 11 (El Segundo), 13 (Belmont Shore), and 15 (Laguna Beach). In September, young seabass settled at the middle stations (stns. 6–11). By October, no new settlement was detected at any of the study sites (Fig. 5). The only YOY white seabass was an older fish (78mmSL) taken at Stn. 16 (San Mateo Pt.).

Sixty-three percent (170 individuals) of all YOY were taken at the 5m depth in 1988. YOY white seabass were most numerous at the 5m isobath at Stns. 2–4, 10–13, and 15, but were more abundant at 10m at Stns. 5–9 (Fig. 6).

Analysis of variance of CPUE values in 1988 indicated that only the observed monthly differences were statistically significant (Table 1). Differences in CPUE among stations and depths were not significant in 1988.

YOY white seabass densities ranged from a low of 0.3 individuals/ha in October 1988, to a high of 37.8 in July 1988. In 1988, population estimates varied greatly along the approximately 300km of coastline (excluding the offshore islands) covered in 1988. Overall density for the 5-month period yielded a population estimate of 130,000 individuals in the area of southern California covered by the sampling.

Summer 1989 Sampling from May to August 1989 along the coastlines of the mainland and the offshore islands produced 85 YOY. The catch rate at the mainland stations was 15 times higher than at island stations (CPUE 0.59/tow in 128 tows vs. 0.04/tow in 240 tows) (Fig. 7). Most (88%) of the YOY were captured at three of the mainland stations: Stns. 6 (Ventura, n 22), 10 (Malibu, n 14), and 15 (Laguna Beach, n 38). Five YOY were captured at Stns. 17 and 18 on Santa Cruz I., four were taken at Stn. 22 (White's Cove) on Santa Catalina I., and none were taken at Santa Rosa or San Clemente I.

The CPUE was low in May (0.14/tow), peaked in June (0.45/tow), and declined through July–August (0.14/tow) (Fig. 8). Settlement was restricted to the southern mainland stations (13 and 15) in May (Fig. 9). By June, settlement was observed as far north as Stn. 6 (Ventura) with the greatest numbers occurring off Stns. 10 (Malibu) and 15 (Laguna Beach). In July and August settlement was highly variable at the mainland stations. The five YOY white seabass taken at Santa Cruz I. (Stns. 17 and 18) were captured during June, July,

Table 1

Summary of three-way ANOVA results for catches of young-of-year white seabass *A. nobilis* during the 1988 and 1989 coastal surveys. Dependent variable in all cases was CPUE. DSTBLK = distance block; * $p<0.05$; ** $p<0.001$.

Test	Effect	df	MS	*F*	*p*
1988 Survey					
Station × Month × Depth	Station	15	0.9832	1.0086	0.4590
	Month	4	5.7207	5.8686	0.0005**
	Depth	1	1.9141	1.9635	0.1663
	S × M	60	1.0263	1.0529	0.4212
	S × D	15	1.3441	1.3788	0.1875
	M × D	4	0.9687	0.9938	0.4180
Error	S × M × D	60	0.9748	—	—
1989 Survey					
DSTBLK × Month × Depth	DSTBLK (DB)	2	2.9712	11.8180	0.0000**
	Month	3	0.6036	2.4008	0.0745
	Depth	1	0.5481	2.1801	0.1440
	DB × M	6	0.4784	1.9029	0.0915
	DB × D	2	0.3110	1.2371	0.2962
	M × D	3	0.7950	3.1623	0.0295*
Error	DB × M × D	74	0.2514	—	—

and August. Stn. 22 (White's Cove, Santa Catalina I.) was the only other Channel Island station where YOY seabass were taken (Fig. 9).

During 1989, 69% (*n* 59) of YOY white seabass were taken at 5m, while 31% (*n* 26) were captured at 10m. Most of the fish taken at the 10m isobath were captured at Stns. 6 (Ventura) and 15 (Laguna Beach). Two YOY white seabass were taken at 10m off Santa Cruz I. (Stns. 17 and 18).

In 1989, catches (CPUE) were then examined according to distance block, month, and depth of capture. Analysis of variance revealed the significant effect of distance block (Table 1; Fig. 10) which was highly significant ($p<0.0001$). Although month and depth were not significant main effects, a significant month-by-depth interaction was detected in the three-way ANOVA. The month-by-depth interaction indicated that depth distributions changed significantly over the period of May–August. Catches of YOY white seabass increased at the 10m depth stratum and decreased at 5m over the course of the summer (Fig. 11).

The population estimate for 1989 based on mean density along ~600km of mainland and offshore islands coastland was about 118,000 individuals over the 4-month sampling.

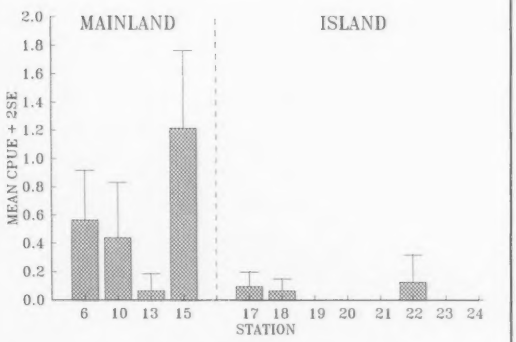


Figure 7

CPUE of YOY white seabass *A. nobilis* by station, summer 1989. Bars represent 2SE of the mean. Stations are grouped into mainland and island sites for comparison.

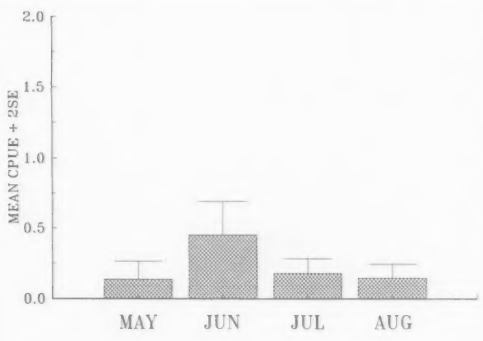


Figure 8

CPUE of YOY white seabass *A. nobilis* by month, summer 1989. Bars represent 2SE of the mean.

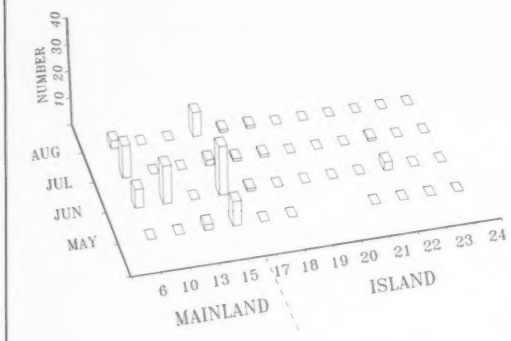


Figure 9

CPUE of YOY white seabass *A. nobilis* by station over the four months (June–October) of the 1989 survey. Stations are grouped into mainland and island sites for comparison. Stns. 19 and 20 (Santa Rosa I.) were not sampled in May due to severe weather conditions.

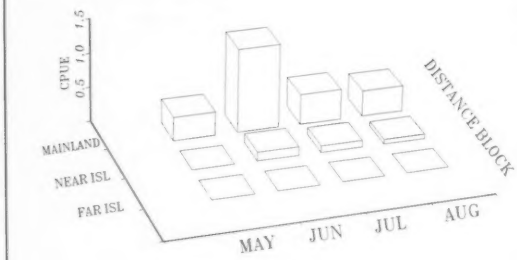


Figure 10

CPUE of YOY white seabass *A. nobilis* within stations grouped by distance block (MAINLAND = four mainland stations, NEAR ISL = four near-island stations, FAR ISL = four far-island stations) over the four months (May–August) of the 1989 survey.

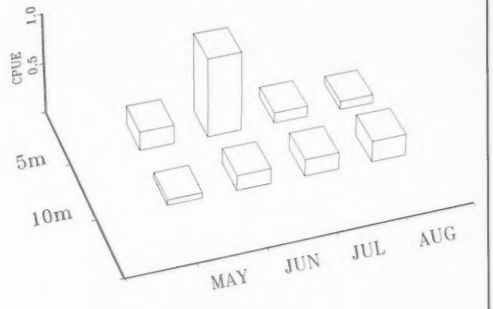


Figure 11

Abundance of YOY white seabass *A. nobilis* by depth over the four months (June–October) of the 1989 survey.

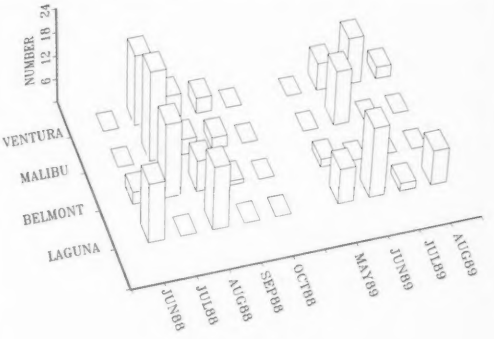


Figure 12

CPUE of YOY white seabass *A. nobilis* at each of four mainland stations by month over the summers of 1988 and 1989. (Stn. 6 = VENTURA, Stn. 10 = MALIBU, Stn. 13 = BELMONT, Stn. 15 = LAGUNA).

Comparison of 1988 and 1989 at four mainland stations

Settlement success in 1988 was compared with that in 1989 by examining the catch at the four mainland stations sampled during both years (Fig. 12). Abundance varied significantly among months over the two summers (one-way ANOVA; F 2.52; 8, 27 df; $p<0.05$), but not among stations. Settlement among the four stations was consistent during 1988, but highly variable in 1989. Also, CPUE was higher in 1988 (0.75/tow) than in 1989 (0.59/tow) but the difference was not significant (t-test; t 1.23; 15 df; p 0.24). Catches differed most between years at Stn. 13 (Belmont Shore) where abundance dropped from 0.78/tow in 1988 to 0.06/tow in 1989, and at Stn. 15 (Laguna Beach) where abundance increased from 0.78/tow to 1.21/tow. The lack of significant differences in catches between 1988 and 1989 was probably due to the high variability and low numbers at individual stations within each year. The relatively high catch at Laguna Beach in 1989 was directly opposed to the lower catches at the other three stations.

Influence of environmental factors

Distance from the mainland Of the environmental variables examined, only the distance of the station from the mainland was significantly correlated with CPUE over both years (Table 2), and this correlation was negative. This corroborates the ANOVA results from 1989 where the effect of distance block was highly

Table 2

Correlation coefficients among catch-per-unit-effort (CPUE) of young-of-year white seabass *A. nobilis* and six environmental variables during the 1988 and 1989 coastal surveys (* $p<0.05$, 219 df).

	CPUE	DSTMN	BTMP	BSAL	BDO	BSLOP	BALGA
CPUE	–						
DSTMN	**−0.2030***	–					
BTMP	0.0993	−0.0115	–				
BSAL	0.0513	−0.0349	−0.0279	–			
BDO	−0.0084	−0.0425	0.0674	−0.0402	–		
BSLOP	0.0967	**−0.3761***	−0.0718	−0.0365	**0.1427***	–	
BALGA	0.0357	−0.0204	−0.0139	−0.0118	−0.0305	−0.1063	–

DSTMN Distance from mainland
BTMP Bottom temperature
BSAL Bottom salinity
BDO Bottom dissoved oxygen
BSLOP Bottom slope
BALGA Biomass algae

significant, further emphasizing the inshore–offshore distribution pattern of white seabass settlement.

Temperature Bottom temperature ranked second among environmental variables in its correlation to CPUE over both years, although the correlation of 0.10 was not statistically significant (Table 2). The lack of significance may be due to the fact that the relationship of catch to temperature differed noticeably in the 2 years and that overall catches were lower in 1989.

In 1988, the heaviest and most widespread settlement of YOY coincided with the striking rise in coastal temperature during July in the study area, resulting in a significant correlation between log-transformed [$\log_{10}$ (x+1)] abundance of YOY and bottom temperature (r 0.25, $P<0.05$, 74 df). In 1989, however, the greatest and most widespread YOY abundance was encountered in June when temperatures were generally depressed. Thus the peak settlement in 1989 occurred 1 month earlier than in 1988 and was apparently not as closely related to a rise in sea temperature as it seemed to be in 1988.

Biomass of drift algae Samples of submerged drift algae ranged from trace amounts (<50 g) to >500 kg per tow for each depth and station. No significant correlation (r 0.036; Table 2) was found between the weight of drift algae and the abundance of young white seabass. However, only two fish (both >60 mm SL) were captured without drift algae in the nets. Thus, drift algae and YOY white seabass may be related on a presence/absence rather than a quantitative basis.

Correlations of catch with other physicochemical variables were too low to warrant consideration.

Multivariate model A combination of three environmental variables—distance from the mainland, bottom temperature, and biomass of drift algae—produced a significant canonical correlation with CPUE (Table 3). Though significant, the correlation accounted for only 5% (R^2 0.052) of the variation in CPUE. A significant canonical correlation with distance and bottom temperature alone accounted for slightly less variation in CPUE (R^2 0.051).

Discussion

Density estimates for white seabass off the coast of southern California were low. Population estimates based on these densities for the Southern California Bight were only 130,000 and 118,000 individuals in 1988 and 1989, respectively. The lower value in 1989 is not surprising since catches at the island stations were extremely low (a high of five YOY at Santa Cruz I., and none at Santa Rosa and San Clemente Is.). Even if these estimates are assumed to be within an order of magnitude of the real population levels, it is obvious that settlement of white seabass was poor in southern California waters. Our data showing relatively low numbers of YOY white seabass in southern California for both sampling years present a similar picture to that presented in Moser et al. (1983) for larval white seabass. The major settlement areas for this species undoubtedly occur to the south in Mexican waters.

Catches of YOY white seabass were highly variable in space and time. Only a small portion of this variability was explained by the environmental variables measured. Monthly differences in catch were marked

Table 3

Results of canonical correlation runs with catch-per-unit-effort (CPUE) of young-of-year white seabass *A. nobilis*, 1988–89, as the dependent variable and selected environmental (independent) variables (* $p<0.05$, ** $p<0.01$).

Successive canonical correlation runs

Run	Variables	Canonical R	Canonical R^2	χ^2	df	P
1	DSTMNLD BTMP BALGA	0.2274	0.0517	11.495	3	0.0093**
2	DSTMNLD BTMP	0.2250	0.0506	11.274	2	0.0036**

Canonical weights within runs

Variables	Run 1	Run 2
DSTMNLD	−0.8848	−0.8973
BTMP	0.4287	0.4312
BALGA	0.1450	

DSTMNLD Distance from mainland
BTMP Bottom temperature
BALGA Biomass algae

in both years, due to the peaks in abundance of YOY observed in both 1988 and 1989, although monthly differences were significant only in 1988. In 1989, a significant spatial pattern of catches was detected, related to distance from the mainland and depth of capture over months.

Both the distance block ANOVA from 1989 data and the overall correlation analyses strongly suggest that the abundance of YOY white seabass decreases rapidly with distance from the mainland. Other factors are less important. Nonetheless, the combination of distance, temperature, and biomass of drift algae produced a highly significant canonical correlation with distance and temperature contributing most heavily to the relationship.

The large amount of unexplained variation in the multivariate model suggests that important factors may be missing from the analysis. We believe that one such factor is the initial availability of presettlement larvae in the plankton. A dearth of premetamorphic larvae at a potential settlement site results in low settlement, no matter how favorable the environmental conditions. Population sizes off southern California might be limited largely by number of settling larvae rather than site-specific environmental factors or density-dependent survival of YOY. Only when larval input is constantly high, as we suspect is the case in Mexican waters, could the influence of environmental factors on settlement success be determined with any precision.

Factors affecting larval availability are not well known. Spawning of white seabass occurs in the summer and may be related to lunar periodicity (moon phase) (Franklin and Allen, unpubl. data) early in the reproductive period. Lunar periodicity of spawning activity coupled with adult stock size, larval transport mechanisms, and larval growth dynamics could all ultimately influence the availability of white seabass larvae.

Distance from the mainland, the strongest correlate with YOY abundance, probably reflects larval availability which may decrease with distance from coastal stocks occurring in both southern and Baja California. Island populations of adults were either not reproducing or their larvae were being carried away from settlement sites. Long-term settlement success of white seabass to islands may be sporadic and highly variable. For example, Cowen (1985) found that California sheephead (*Semicossyphus pulcher*) settled only sporadically to the offshore islands. The pattern of settlement success of sheephead over a 7–9 year period in areas without larval sources "upstream" of typical current direction was highly variable and dependent on episodic events, such as the El Niño climatic anomaly (Cowen 1985).

Warm water currents may be important to white seabass settlement for two reasons: (1) Large numbers of larvae carried northward from more southern waters by warm water currents may settle after metamorphosis and locate suitable habitat; and (2) the warm water itself may induce locally spawned larvae to settle. On a larger scale, major water movements such as the California Current, gyral circulation ("eddies"), and other mesoscale flows (e.g., internal waves) may

control white seabass settlement in the Southern California Bight. Parrish et al. (1981) demonstrated that seasonal effects of the California Current and upwelling in central California had a major effect on the distribution patterns of marine fish. The spawning activities of most fishes coincide with the onshore flow which is characteristic of the late winter and early spring months and transports eggs and larvae into shallow waters. The effects of major hydrographic events on the abundance and distribution of YOY white seabass remain largely unknown.

The main geographic source of white seabass larvae that settle successfully in southern California is also unknown. Southern California populations of adults may be reduced to the point that they may be only a minor source of larvae. Since larvae remain in the plankton as long as 4–5 weeks, population centers of adults off northern Baja California may constitute the major source of southern California YOY seabass. Thus, successful settlement to southern California waters may depend largely on the northward-flowing, warm-water currents best developed in the summer months. Satellite infrared-imagery data indicated that such a large, warm-water mass moved north along the southern California coastline in early July 1988 (Jan Svedkowsky, Ocean Imaging, San Diego, pers. commun.). The resulting dramatic rise in surface and bottom temperatures may have accounted for the marked increase in settlement of white seabass between June and July of that year if the water mass also contained a sufficient number of premetamorphic larvae. Studies of subpopulation structure utilizing restriction fragment length polymorphism (RFLP) analysis of nuclear DNA are currently underway in our laboratory in an attempt to identify the source of newly-settled white seabass in southern California coastal waters. If the main parental population of these fish is located in more southerly waters, joint U.S. and Mexican management efforts may be necessary to prevent the decline of these major breeding stocks in the south.

Acknowledgments

A study of this magnitude could not have been accomplished without the support of many people. We thank those who ably assisted with the demanding field work, especially Jan Cordes, Monica Lara, Julia Sears-Hartley, Phyllis Travers, and Lisa Wooninck. The crew of the RV *Yellowfin*, Jim Cvitanovich, Danny Warren, and Dennis Dunn, assisted greatly through their capable handling of vessels in shallow and often turbulent waters. Al Ebeling and three anonymous reviewers greatly improved this paper through careful readings and numerous, helpful comments. We also gratefully acknowledge the assistance provided by Steve Crooke and Paul Gregory of the California Department of Fish and Game. This research was supported through contracts with the Ocean Resource Enhancement and Hatchery Program (OREHP) and the Bay, Estuarine, and Nearshore Ecosystem Studies (BENES) program, administered by the California Fish and Game.

Citations

Allen, L.G., and M.P. Franklin
1988 Distribution and abundance of young-of-the-year white seabass (*Atractoscion nobilis*) in the vicinity of Long Beach harbor, California, 1984–1987. Calif. Fish Game 74:245–248.

Cowen, R.K.
1985 Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: Causes and implications. J. Mar. Res. 43:719–742.

Donohoe, C.
1990 Distribution, abundance, food habits, age determination, and growth, of late larval and early juvenile white seabass, *Atractoscion nobilis*, off San Diego County, Calif. Unpubl. master's thesis, Calif. State Univ., San Diego, 95 p.

Frey, H.W. (editor)
1971 California's living marine resources and their utilization. Calif. Dep. Fish Game, Sacramento, 148 p.

Margulies, D.
1989 Size-specific vulnerability to predation and sensory system development of white seabass, *Atractoscion nobilis*, larvae. Fish. Bull., U.S. 87:537–552.

Miller, D.J., and R.N. Lea
1974 Guide to coastal marine fishes of California. Calif. Fish Game, Fish Bull. 157:1–249.

Moser, H.G., D.A. Ambrose, M.S. Busby, J.L. Butler, E.H. Sandknop, B.Y. Sumida, and E.G. Stevens
1983 Description of early stages of white seabass, *Atractoscion nobilis*, with notes on their distribution. Calif. Coop. Oceanic Fish. Invest. Rep. 24:182–193.

Parrish, R.H., C.S. Nelson, and A. Bakun
1981 Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1:175–203.

Vojkovich, M., and R. Reed
1983 White seabass, *Atractoscion nobilis*, in California–Mexican water: Status of the fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 24:79–83.

Depth, capture time, and hooked longevity of longline-caught pelagic fish: Timing bites of fish with chips

Christofer H. Boggs

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396

Abstract.—To resolve the uncertainty in estimating capture depths of fish on pelagic longline gear, electronic microchip hook timers were attached to branch lines to record when bites occurred, and time-depth recorders (TDRs) were attached to longline gear, off Hawaii in January 1989 and January–February 1990. Hook timers indicated that 32% of the striped marlin *Tetrapturus audax*, 21% of the spearfish *T. angustirostris*, and 12% of the bigeye tuna *Thunnus obesus* were caught on sinking or rising hooks, demonstrating that capture time data are needed to correctly estimate capture depth. Recorded and predicted longline depths differed greatly, indicating that TDRs are essential for describing depth distributions of fish from longline catches. Most (>60%) of the spearfish and striped marlin were caught on settled hooks (not sinking or rising) at depths of <120 m, whereas most bigeye tuna were caught at depths of >200 m. This suggests that eliminating shallow hooks could substantially reduce the bycatch of spearfish, striped marlin, and other recreationally important billfish without reducing fishing efficiency for bigeye tuna. Bigeye tuna and striped marlin survived up to 6–9 hours after capture, and over 50% of 12 frequently-caught taxa were alive when retrieved, suggesting that the release of live fish can be an effective management option.

Manuscript accepted 5 May 1992.
Fishery Bulletin, U.S. 90:642–658 (1992).

Targeting specific depths can improve longline catches of desired species, such as bigeye tuna *Thunnus obesus* (Saito 1975, Hanamoto 1976, Suzuki et al. 1977, Suzuki and Kume 1982), and reduce bycatch of other species, such as billfish (Suzuki 1989). However, considerable uncertainty exists in estimating the fishing depth of longline gear. Predicted longline depth based on catenary geometry, line length, and distance between floats (Yoshihara 1954) differs from true depth (Saito 1973, Hanamoto 1974, Nishi 1990) because of currents and other factors, yet depth is often inferred rather than measured (Suzuki et al. 1977, Suzuki and Kume 1982, Hanamoto 1987, Grudinin 1989). Furthermore, fish may be caught while the hooks are sinking, during deployment of the gear, or rising during its retrieval (Saito 1973), making capture depths impossible to estimate accurately without known capture times.

Accurate estimates of fishing depth can be made if time-depth recorders (TDRs) are attached to longline gear. Longline studies using TDRs (Saito et al. 1970, Saito 1973, Yamaguchi 1989, Nishi 1990) have also interpreted TDR depth fluctuations as records of times of capture, but few such measurements exist. Instead, capture has been assumed to occur when the gear is settled, so capture depth has been estimated as settled hook depth (Hanamoto 1976, Suzuki and Kume 1982). Hook timers, designed to indicate when each hook is struck (Somerton et al. 1988), provide a way to measure capture times and survival times of hooked fish. Capture times, together with TDR records, can be used to estimate capture depths accurately.

Billfish catch rates in recreational fisheries may be negatively affected by nearby longline fisheries (Squire and Au 1990), and interest in finding ways to reduce the longline take of billfish without reducing fishing efficiency for target species is increasing (Rockefeller 1989). Information on capture depth, capture time, and hooked longevity can be used to design fishing methods that reduce billfish mortality. Data on the selectivity and efficiency of longline gear at various depths are also critical for stock assessments (Suzuki 1989).

The present study improves methods for estimating capture depths of fish on longline gear using electronic timing devices, and describes the depth distributions and capture times of tunas, billfishes, sharks, and other pelagic fishes in Hawaiian waters in winter. Water temperature and dissolved oxygen (DO) were measured to describe the physical habitat in the study area, since these variables appear to cause geographic variation in depth distributions of fish (Hanamoto 1975, 1987). Relative fishing efficiency and the bycatch of billfish were predicted for several gear configurations.

Table 1

Summary of longline fishing operations conducted by the NOAA ship *Townsend Cromwell* off Hawaii, January 1989 and January–February 1990, giving averages for three set types (ranges in parentheses). Baskets were intervals of continuous main line between floats with snap-on branch lines, not spliced units of gear. Shortening rate was the ratio between ship speed and thrower speed. Depths do not include branch line length. Predicted depths were calculated from the shortening rate and the main line length per basket, assuming a catenary shape. TDR = time depth recorder.

Year	Set type	Sets (no.)	Time		Hooks per set (no.)	Line per basket (m)	Shortening rate (ratio)	Predicted depth (m)	Deep TDR depth (m)	Middle TDR depth (m)
			Begin set	End retrieval						
1989	Regular	6	8:09 (4:31–10:05)	15:24 (14:20–16:41)	199 (128–278)	795 (640–1103)	0.80 (0.69–0.98)	222 (88–304)	111[1] (43–180)	82[2] (32–133)
	Deep	6	8:55 (5:29–12:47)	16:36 (10:34–20:40)	257 (185–392)	1085 (990–1146)	0.59 (0.46–0.83)	415 (273–489)	260 (241–303)	191[2] (178–224)
	Very deep	4	8:23 (8:16–8:41)	19:10 (17:58–20:40)	405 (356–474)	1117 (1053–1146)	0.54 (0.45–0.71)	447 (349–496)	367 (329–400)	270[2] (243–295)
1990	Regular	5	6:50 (6:14–7:18)	19:08 (16:24–22:07)	456 (212–591)	809 (611–1068)	0.78 (0.67–0.90)	243 (150–355)	142 (78–183)	104 (71–140)
	Deep	13	7:18 (6:12–10:04)	19:38 (17:57–20:42)	474 (173–594)	1069 (798–1265)	0.60 (0.40–0.70)	409 (298–499)	249 (193–318)	180 (122–232)
	Very deep	4	5:29 (4:45–6:21)	19:03 (15:30–21:05)	404 (219–600)	1165 (937–1427)	0.62 (0.50–0.74)	436 (303–592)	416 (340–517)	291 (251–381)

[1]TDR data obtained for only three sets.
[2]Calculated from the ratio (0.73) between middle and deep TDR depths of sets in which middle-position data were available.

Materials and methods

Longline fishing was conducted on board the NOAA ship *Townsend Cromwell* in January 1989 and January–February 1990. Sets were made between lat. 14° and 20°N, long. 148° and 159°W, 20–500 nmi from the main Hawaiian Islands, and within an area typically fished by Hawaii's domestic longline fishery. Gear was usually deployed in the morning and retrieved in the afternoon or evening (Table 1), or occasionally at midday to permit a second set on the same day. No sets were made at night. Except for the hook timers and TDRs, the fishing gear and operations were similar to commercial longline fishing methods for tuna in Hawaii (Kawamoto et al. 1989) prior to the advent of night fishing for swordfish *Xiphias gladius*. Both this study and the contemporary commercial longline fishery used a wide variety of fishing depths. Commercial fishermen used more gear (~1000 hooks), let it stay in the water longer (~12 h), and retrieved it faster than in this study.

The fishing gear consisted of 3.5 mm-diameter nylon monofilament main line deployed with a line thrower (Kawamoto et al. 1989). The main line was supported at intervals by vertical, 18 m lines with floats at the ends. Snap-on branch lines made of 2.1 mm-diameter clear-blue nylon monofilament (20 m long in 1989 and 11 m long in 1990) were baited with thawed saury *Cololabis saira* on curved tuna hooks (one hook/branch line) and attached to the main line between float lines. Hooks were size 3.6 (Japanese size is 10.9 cm from eye to point). Each portion of the longline between floats and the attached branch lines constituted a "basket," a term taken from older gear in which the number of branch lines is fixed. However, this study used varying numbers of snap-on branch lines (12, 14, 16, or 20/basket), depending on the length of main line per basket.

Hook position was controlled by timing the attachment of branch lines as the main line was thrown overboard mechanically at a controlled speed. A computer program was used to signal and record attachment times. Deviations from the programmed instructions were noted, providing a record of set times for each hook. The total number of hooks in each set was 128–600, and the amount of main line deployed per set was 9–44 km (Table 1). The amount of gear increased with crew experience but also varied because of inclement weather and equipment failures.

Set depths

Fishing depth was altered by varying the slack in the main line and the length of line per basket (Table 1) and by exogenous factors such as wind and currents. Line slack was quantified as the shortening rate (Saito 1973), or sagging rate (Suzuki et al. 1977), equal to the horizontal distance between floats divided by the length of line per basket (a dimensionless ratio). At deploy-

ment, the shortening rate was the same as the ratio of ship speed through the water to line-thrower speed: 0.40 (maximum slack) to 0.98 (no slack). The length of main line per basket was 640–1427 m. The predicted maximum depth of the main line during each set was calculated from the shortening rate and the main line length per basket (Table 1), assuming a catenary shape (Yoshihara 1954).

The depth of each set was recorded with electronic TDRs (Wildlife Computers, models MKII and MKIII) programmed to sample depth once per minute. The TDRs were attached at the deep positions, defined as the attachment points for the branch line midway between floats (e.g., position 10 or 11 of 20 between floats). In 1990, TDRs were also attached at the middle positions between the deep positions and the float line (e.g., at position 5 or 15 of 20 between floats).

The time that the gear took to sink during deployment (0.5 h) and to rise during recovery (0.5 h) was quantified from TDR records. Set depth was described as the typical depth observed in records from the deep-positioned TDRs during the period after sinking and before rising. Recorded depth was examined after each set and compared with predicted depth. Shortening rate, the length of line per basket, or both were adjusted in the subsequent set to reach targeted depths.

Hook depths

The settled depth of each attachment point for the branch line was estimated by interpolating between (1) the TDR record for the deep and middle positions or (2) the latter point and the shallowest depth of the main line (assumed to equal the length of the float line). Settled hook depth was calculated by adding the branch line length to the interpolated depth of the branch line snap. Not enough TDRs were available (2 in 1989, 10 in 1990) to put 1 TDR on every basket. When fish were caught by baskets without TDRs, average TDR depths for that set were used to interpolate settled hook depths. For middle positions without TDRs in 1989, depth was estimated from the mean ratio of the middle position to deep-position TDR depths based on 1990 data.

Hook timers

Hook timers were made of a plastic resin cast around a battery-powered microchip clock controlled by a magnet (Somerton et al. 1988). They were attached to the branch lines near the snap, bridging a bend in the line (Fig. 1). A fish striking the hook pulled the magnet, thus triggering the timer. In 1989, a rubber band held the magnet in place against a test weight of about 1–2 kg. In 1990, thread with a breaking strength of 4–5 kg bridged the bend in the line, and the magnet was held in place by a weaker thread until the bridging thread was broken (Fig. 1). Some branch lines were set without timers (14% in 1989, 35.5% in 1990) to preclude interruptions in fishing when timers were tangled or otherwise unavailable.

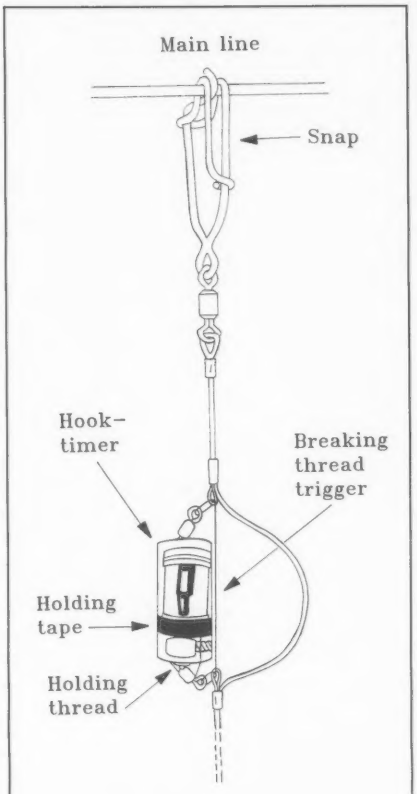


Figure 1
A hook timer and its trigger mechanism as arranged in 1990, when thread triggers were used. In 1989, rubber bands served as the trigger. The slack loop in the branch line was pulled taut when a fish struck the hook, breaking the trigger and pulling the magnet from its recess in the bottom of the hook timer.

Hook timers indicated elapsed time in whole minutes (e.g., 0 min indicated 0–59 s). Timers were read as the branch lines were recovered, or soon after, with corrections made for delays. Timers were categorized as being triggered (1) at recovery (≤ 1 min before removing the branch line snap), (2) while rising (>1 min–0.5 h before recovery), (3) while settled (>0.5–<1.0 h, 1–<2, 2–<3 h, and so on before recovery), (4) while

sinking (<0.5 h after gear deployment), (5) at deployment (≤2 min after deployment), and (6) before deployment (timer triggered before setting commenced). Timers activated but without fish were categorized similarly except all settled categories (>0.5–9.0 h) were combined. Untriggered hook timers with fish also were tallied, and hooks with timers that were damaged, broken loose, or tangled too badly to be triggered were counted as hooks without timers.

The numbers of fish caught while the gear was sinking, settled, and rising were summarized. The unconfirmed depth of capture of each fish was defined as the settled depth of the hook. Capture depths were considered confirmed only if hook timers indicated the capture occurred within the period in which the gear was settled.

Catch and effort

Live fish that were not needed as specimens were tagged and released. Steel head "H" type dart tags (Squire 1987) were applied using a 3 m tagging pole while the fish remained in the water. Billfish were also injected with 5–20 mg oxytetracycline/kg of fish using pole-mounted syringes (Foreman 1987) to mark hard parts for validation of growth increments. Fish were released by cutting the branch lines close to the hooks with a tree-trimming pole. The condition (alive or dead) of the retained fish was noted, and it was weighed to the nearest 0.5 kg or measured to the nearest 0.1 cm. For the five most-frequently-caught species of commercial importance, catch, number of hooks, and number of hooks with timers were stratified into 40 m strata (40–<80 m, 80–<120 m, and so on) based on settled hook depths. The catch-per-unit-effort (CPUE) in each depth stratum was examined in two ways: (1) by confirmed capture depth ($CPUE_D$ in number of fish/1000 hooks with timers) representing the depth distribution of fish; and (2) by settled hook depth ($CPUE_H$ in number of fish/1000 hooks), representing the total effectiveness of hooks while sinking, settled, or rising.

The $CPUE_H$ for each depth was used to predict catch rates of "standardized" types of gear to illustrate the use of catch by hook position in estimating relative gear efficiency for different gear configurations. Total CPUE for each standardized gear configuration was estimated by calculating the weighted average $CPUE_H$, with weights corresponding to a given number of hooks per depth stratum for each configuration. Total CPUE was calculated from 1989 and 1990 data separately and averaged. Gear efficiency was calculated as the ratio of the predicted CPUE for each configuration to that of the regular configuration.

Standardized regular and deep longline gear configurations were assumed to have 6 and 13 hooks/basket, respectively. A shortening rate of 0.6 and the dimensions in Suzuki et al. (1977; without adjustment for currents) indicated hook depths of about 95, 140, and 170 m (for regular gear) and 100, 145, 190, 230, 265, 290, and 300 m (for deep gear). These depths correspond roughly to the midpoints of hook depth strata in the present study (100, 140, 180, 220, 260, and 300 m).

In addition to regular and deep gear, CPUE values for two hypothetical gear types were predicted: (1) shallow gear for which hooks are limited to the first three depth strata of this study; and (2) a proposed new gear for which no hooks would be deployed in the first three depth strata and the distribution of deeper hooks would match that of deep gear. The shallow gear configuration may be representative of that achieved by Hawaii's longline fishermen in 1989 and 1990 when they first began using monofilament longline and had difficulty achieving the depths formerly fished with traditional rope gear. With the rope gear, slack was obtained by manually throwing the baskets with the main line partially coiled. The [predicted] CPUE for the new gear type was estimated to indicate the reduction in bycatch of some species by the elimination of shallow hooks.

To show CPUE as it would appear in a study of gear configurations without hook position, capture depth, or capture time information, $CPUE_S$ values were calculated from catch and effort by set type. Sets were categorized on the basis of depth (TDR depth plus branch line length) into three groups: 60–<200 m (regular), 200–<330 m (deep), and 330–530 m (very deep). The first two groups contained depth ranges roughly comparable to those expected for regular and deep longline gear types, assuming a variety of shortening rates and variation due to ocean currents (Suzuki et al. 1977).

Oceanography

Vertical temperature structure in the area of each set was measured by expendable bathythermographs (XBTs; 400 m depth) and conductivity-temperature-depth casts (CTDs; 500–1000 m depth, usually 500 m) before or after each set. Water samples were taken with Niskin bottles to measure DO and to calibrate DO measurements made by CTDs.

Many of the TDRs were equipped with a second channel to record temperature. The TDRs were attached to the CTD probe to calibrate depth and temperature measurements. The TDR temperature data were used to estimate set depths exceeding 400 m (the lower limit for accurate range depth measurement from the TDRs).

Table 2

Catch data for 14 frequently-caught taxa in research longline sets off Hawaii, January 1989 and January–February 1990. Some weights were calculated from length measurements; some fish (i.e., those released) were not weighed.

Species	No. caught	No. weighed or measured	Weight (kg)		Alive (%)
			Average	Range	
Bigeye tuna *Thunnus obesus*	76	32	31.5	2.5–69.5	83
Yellowfin tuna *T. albacares*	16	11	39.5	7.5–62.5	63
Skipjack tuna *Katsuwonus pelamis*	5	5	9.0	7.0–11.0	20
Wahoo *Acanthocybium solandri*	4	3	17.5	7.5–25.0	0
Striped marlin *Tetrapturus audax*	67	20	18.0	9.5–37.0	71
Spearfish *T. angustirostris*	41	23	13.5	8.5–18.5	56
Mahimahi *Coryphaena hippurus*	90	60	6.5	2.5–16.0	88
Pomfrets (Bramidae)	17	15	5.5	2.0–10.0	86
Lancetfish *Alepisaurus ferox*	132	111	1.5	0.1–8.0	64
Ribbonfish *Trachipterus ishikawae*	4	2	8.0	7.0–8.0	75
Brown ray *Dasyatis violacea*	8	4	2.0	1.0–2.5	88
Whitetip shark *Carcharhinus longimanus*	26	—	—	—	85
Blue shark *Prionace glauca*	21	1	68.0	—	100
Thresher shark *Alopias* spp.	6	1	91.0	—	60

Results

A total of 16 longline sets caught 149 fish in 1989 and 22 sets caught 401 fish in 1990. Fishing effort totaled 14,410 hooks including 10,236 hooks with timers. There were 14 taxa for which more than 3 fish were caught (Table 2).

Achieving deep sets when intended was sometimes difficult. Backlash of the main line into the hydraulic line thrower created problems at high thrower speeds, and ship speed through the water was sometimes underestimated, reducing the shortening rate. Wind and currents reduced set depth by dragging floats and parts of the line in opposing directions. In particular, current shear between the surface and the waters below the thermocline, observed with an acoustic Doppler current profiler, seemed to prevent deep sets. Observed set depths were highly variable and usually less than the predicted depths (Table 1, Fig. 2). For example, at a predicted depth of about 490 m, observed depths were 200–400 m (Fig. 2). Sets averaged only 54% and 68% of the predicted depths in 1989 and 1990, respectively. For the first three sets in 1989, the TDRs failed, so depth was estimated as a percentage of the predicted depth based on the average percentage (49.3%) obtained from the next three sets with similar configurations.

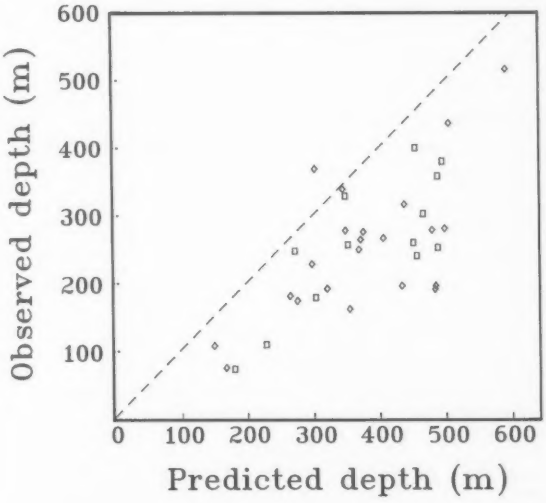


Figure 2

Relationship between predicted and observed set depths in 1989 (□) and 1990 (◇). Observed depths were measured with time-depth recorders, and predicted depths were calculated from the shortening rate and the main-line length per basket, assuming a catenary shape.

Capture depths

Capture depths were confirmed for those fish caught >0.5 h after deployment and >0.5 h before retrieval, because the TDR records showed that the main line usually took 0.5 h to sink to within about 90% of its settled depth and about 0.5 h to rise to the surface during retrieval (Fig. 3). Records of settled depth sometimes varied ≤100 m for the deep sets (e.g., set 14;

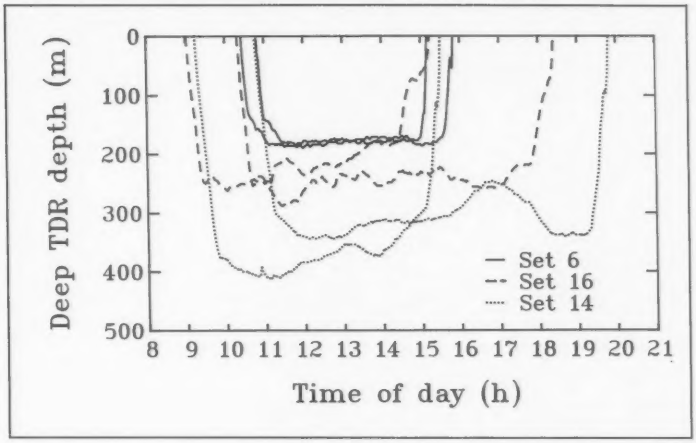


Figure 3 (left)
Sample records from time-depth recorders (TDRs) measuring the deep positions on three sets (each with two TDRs) in 1989, illustrating the typical sinking time (0.5 h), variation in settled depth, and typical rising time (0.5 h).

Figure 4 (below)
Hook depths for catches of 14 frequently-caught taxa in a study off Hawaii, winter 1989 and 1990 (combined). Settled hook depths are shown for all hooks that caught fish (unconfirmed) and for those hooks that caught fish while settled (i.e., not sinking or rising) as indicated by hook-timer data (confirmed).

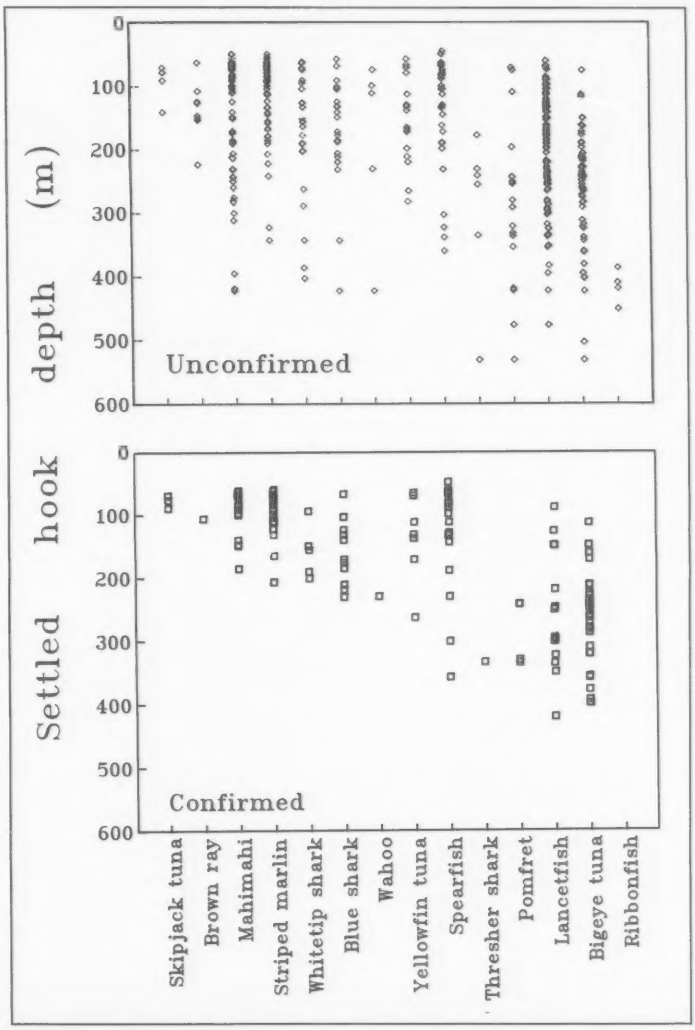


Fig. 3) and ⩽40 m for the regular sets. Also, the gear sometimes took more than 0.5 h to rise (e.g., the first TDR on set 16; Fig. 3) or sink. Such deviations contributed to the variation in estimated capture depths. Capture depths of fish caught with hook timers on baskets with TDRs were based on the TDR depth at the time of capture; however, most catches were made by baskets without TDRs.

A comparison between the unconfirmed depths of all hooks that caught fish and those confirmed to have caught fish while settled (Fig. 4) showed that without hook-timer confirmation, many fish appeared to be caught at greater depths than they actually were. For example, mahimahi *Coryphaena hippurus* had unconfirmed capture depths of ⩽420 m and confirmed capture depths of <190 m. Most confirmed capture depths were <100 m for mahimahi and skipjack tuna *Katsuwonus pelamis*. Striped marlin *Tetrapturus audax*, whitetip shark *Carcharhinus longimanus*, blue shark *Prionace glauca*, and wahoo *Acanthocybium solandri* had unconfirmed depths of ⩽350–420 m and confirmed depths of <200–230 m. Species having a preponderance of confirmed capture depths of <150 m were yellowfin tuna *Thunnus albacares*, striped marlin, and spearfish *Tetrapturus angustirostris*. Most confirmed capture depths were >200 m for thresher

shark *Alopias* spp., pomfrets (Bramidae; species included *Taractichthys steindachneri, Taractes rubescens, and Eumegistus illustris*), lancetfish *Alepisaurus ferox*, and bigeye tuna (Fig. 4).

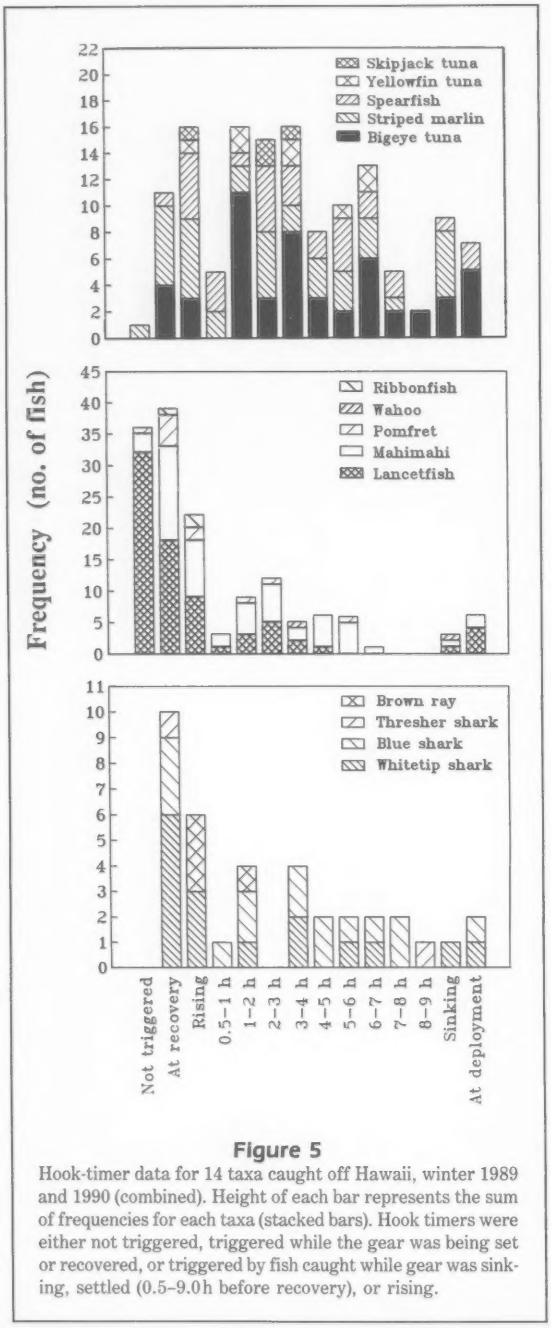


Figure 5

Hook-timer data for 14 taxa caught off Hawaii, winter 1989 and 1990 (combined). Height of each bar represents the sum of frequencies for each taxa (stacked bars). Hook timers were either not triggered, triggered while the gear was being set or recovered, or triggered by fish caught while gear was sinking, settled (0.5–9.0 h before recovery), or rising.

Capture times

Most of the fish (except ribbonfish *Trachipterus ishikawae* and brown ray *Dasyatis violacea*) were caught

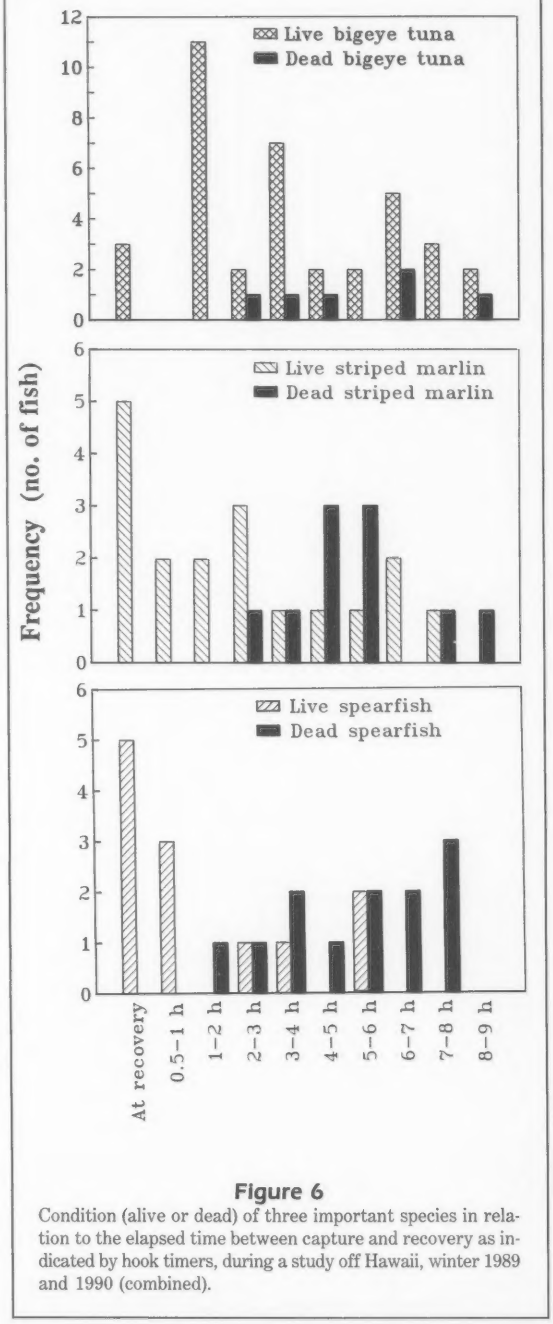


Figure 6

Condition (alive or dead) of three important species in relation to the elapsed time between capture and recovery as indicated by hook timers, during a study off Hawaii, winter 1989 and 1990 (combined).

while the gear was settled rather than while it was sinking or rising (Fig. 5), probably because the gear spent much more time in the settled position. However, substantial numbers of mahimahi, billfish, and other species were caught while the gear was rising (Fig. 5), which explains how fish were caught on deep-positioned hooks (unconfirmed depths) when their confirmed depth distribution was shallow (confirmed depths; Fig. 4).

For many species, catch-per-unit-time (CPUT) may have been highest while the gear was rising. The CPUT values at <3 and ≥3 h before recovery were not directly comparable because short sets resulted in lower effort (number of hooks with timers) ≥3 h before recovery. The catch in the 1–2 h and 2–3 h periods (Fig. 5) must be divided by 2 for comparison with the CPUT in the 0.5 h and 0.5–<1.0 h periods. For periods of 0.5–1.0, 1–2, and 2–3 h before recovery, CPUT values were less than during the rising period for ribbonfish, pomfrets, mahimahi, lancetfish, striped marlin, spearfish, brown ray, and whitetip shark (Fig. 5). In contrast, the values for yellowfin and skipjack tunas were not much different between settled and moving gear and were highest for bigeye tuna 1–2 h and 3–4 h before recovery. Blue shark CPUT values were highest 1–2 h before recovery.

Relatively large numbers of fish were categorized as caught at recovery (Fig. 5). However, estimates of the delay between recovery and reading each timer were not precise (± 1 minute). Thus some fish caught "at recovery" actually had timers triggered after recovery. Hook timers that did not catch fish were most often triggered "at recovery" (Table 3), suggesting that handling activated the timers. A similar lack of precision affected capture times "at deployment."

Hooks with timers triggered by small fish or without catching fish may have resulted in false capture times if larger fish were caught later on those hooks. Fortunately, small (<10 kg) fish, particularly lancetfish (Table 2), were most frequently caught without triggering the timers (Fig. 5). It was unusual for larger (~10–90 kg) fish, such as tunas, billfishes, or sharks (Table 2, Fig. 5), to be caught without triggering the timers. The increase in breaking strength of the triggers in 1990 (Fig. 1) decreased the relative number of small fish that triggered timers, and reduced the proportion of timers triggered without catching fish from 18.5% in 1989 to 9.7% in 1990 (Table 3).

Survival and release

Over 56% of the fish other than wahoo and skipjack tuna were alive when recovered, and for most species, survival was higher than 70% (Table 2). Based on fish with hook-timer data, over half of the bigeye tuna recovered up to 9 h after capture were alive. None of the 11 bigeye tuna recovered 1–2 h after capture were dead, and the shortest period between capture and recovery of dead bigeye tuna was 2–3 h (Fig. 6). Striped marlin were less hardy, with over half recovered dead ≥3 h after capture; nevertheless, many were recovered alive up to 6–8 h after capture (Fig. 6). Spearfish were the least hardy: The longest survival time was 5–6 h, and dead fish were recovered at <1–2 h after capture (Fig. 6).

Of the 29 bigeye tuna, 35 striped marlin, and 11 spearfish tagged during the study, 2 bigeye tuna and 1 striped marlin were recaptured 3–10 months later. These three fish were tagged after having been on branch lines for 3–6 h. The marlin had been injected

Table 3

Frequencies of activated hook timers on branch lines without fish (as percentage of total timers) categorized by elapsed time since the timers were triggered (range of values from individual sets in parentheses).

	Elapsed time							
	Before retrieval			After deployment				
Year	At retrieval (≤1 min)	Rising (>1–30 min)	Settled (≥30 min)	Sinking (≤30 min)	At deployment (≤2 min)	Activated before deployment	No. timers	Branch lines with timers (%)
1989	6.4 (—)*	1.2 (0–3.2)	3.9 (0.8–7.1)	1.0 (0–5.7)	4.8 (1.6–7.1)	1.0 (0–3.3)	3744 (126–356)	86.0 (61–100)
1990	3.8 (1.1–6.2)	1.5 (0–4.8)	2.6 (0.8–6.5)	0.4 (0–1.1)	1.0 (0–2.6)	0.4 (0–2.4)	6492 (167–418)	64.5 (34–99)
Combined	4.7*	1.4	3.1	0.6	2.4	0.6	10236	71.0

* Number recorded only during the first set in 1989. To calculate the combined frequency (4.7%), frequency was assumed to be 6.4% throughout 1989.

with 6 mg/kg oxytetracycline, but no flourescent mark was found in the otolith or vertebrae.

Abundance in relation to depth

For bigeye tuna, the depth distribution of $CPUE_D$ values (number of fish/1000 hooks with timers) was similar in 1989 and 1990, with $CPUE_D$ highest at 360–400 m and relatively high at 200–400 m (Fig. 7). Hooks with timers triggered before or at deployment could not be subsequently triggered; therefore, they were counted as hooks without timers when $CPUE_D$ was calculated (Table 4). The data from wider depth ranges in both years were pooled to obtain sample sizes (number of hooks with timers; Table 4) large enough to determine whether significant differences existed between depths (Fig. 8). For bigeye tuna, $CPUE_D$ values were significantly higher at depths of >200 m than at depths of <200 m ($P<0.05$, based on 95% CI for the difference between proportions). Few (12%) of

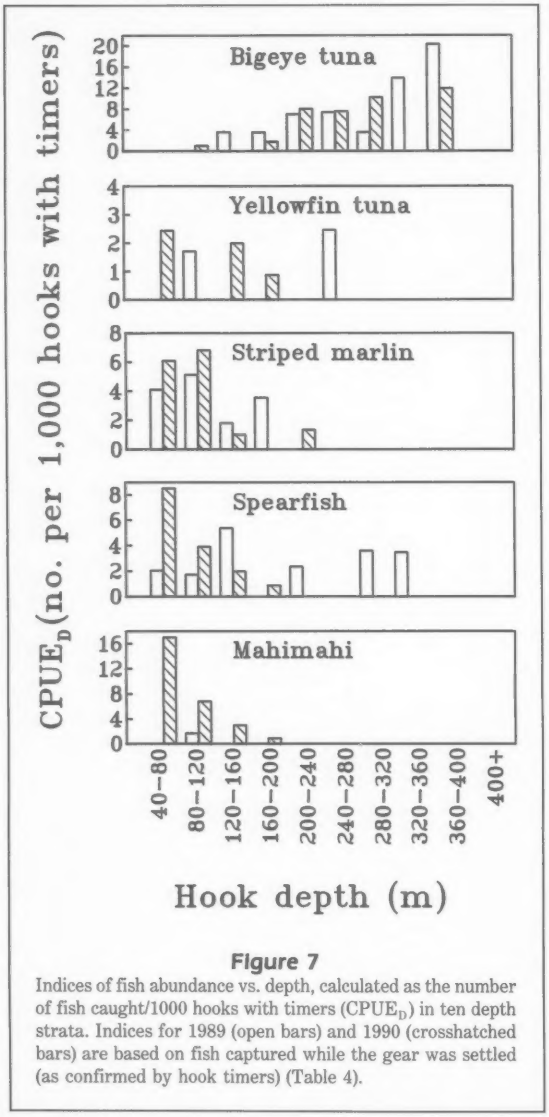


Figure 7

Indices of fish abundance vs. depth, calculated as the number of fish caught/1000 hooks with timers ($CPUE_D$) in ten depth strata. Indices for 1989 (open bars) and 1990 (crosshatched bars) are based on fish captured while the gear was settled (as confirmed by hook timers) (Table 4).

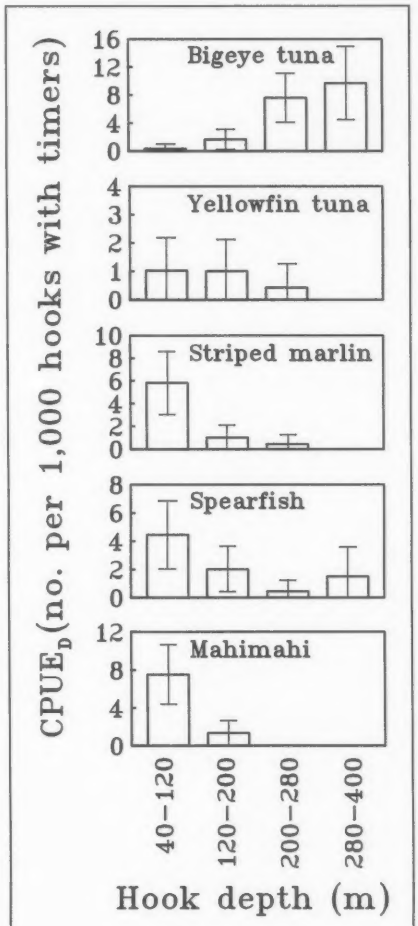


Figure 8

Indices of fish abundance vs. depth, calculated as the number of fish caught/1000 hooks with timers ($CPUE_D$) in four pooled hook-depth strata. Indices for 1989 and 1990 combined are based on fish captured while the gear was settled (as confirmed by hook timers) (Table 4). Error bars indicate 95% CI of the $CPUE_D$ values for each depth category.

the bigeye tuna with hook timers were caught while the hooks were moving (sinking or rising; Table 4). No clear relationship existed between depth and the proportion caught on moving hooks (Table 4).

Yellowfin tuna were not very abundant, which is typical for the winter months off Hawaii. The $CPUE_D$ for yellowfin tuna was not the same in both years (Fig. 7), but the number of fish caught with timers was very small, particularly in 1989 (Table 4). Pooled $CPUE_D$ was highest at 40–200 m (Fig. 8) although no significant difference in $CPUE_D$ by depth was found. The 40 m end of the depth range did not indicate the shallowest depths preferred by any species, since no hooks fished depths of <40 m.

Timer-confirmed catches by settled hooks indicated the highest catch rates for striped marlin were at 40–120 m in both years (Fig. 7), and pooled $CPUE_D$ was clearly the highest at this depth range (Fig. 8). The overall proportion of striped marlin caught on moving hooks was high (32%; Table 4) and increased with depth. At >120 m most striped marlin were caught by moving hooks, and at >200 m only one was caught by a settled hook (Table 4).

For spearfish, the pattern of $CPUE_D$ vs. depth differed between years. In 1989, the highest $CPUE_D$ was at 120–160 m although several fish were caught as deep as 280–360 m; however, in 1990 the highest $CPUE_D$ was at 40–80 m, and no confirmed capture depths were recorded at >200 m (Fig. 7). Pooled data suggested that spearfish were more abundant at <120 m, but the $CPUE_D$ at 40–120 m was not significantly different from that at 120–200 m (Fig. 8). In 1989, a large proportion (43%) of the spearfish were caught on moving hooks, but none were caught on moving hooks in 1990 (Table 4). Furthermore, for each of the major species, a higher proportion of fish were caught on moving hooks in 1989 than in 1990 (Table 4). An early report (Boggs 1990) on this research was based on 1990 data (Table 4) wherein only 12% of the tuna and billfish (combined) were caught on moving hooks.

Table 4

Catch of five commercially-important species in research longline sets off Hawaii, 1989 and 1990, giving fishing effort (number of hooks and timers) by depth strata, number caught (*N*) on known hook position, number confirmed by timers to be caught on moving (M; i.e., sinking or rising) and settled (S) hooks (in parentheses), and percentage of fish caught on moving hooks. Depth ranges include branch line length. Timers do not include those triggered at or before deployment. Catch totals are sometimes less than in Table 2 and Figure 5 because hook number and depth were not known for a few fish.

Hook depth (m)	Year	Hooks in stratum	Timers in stratum	Bigeye tuna		Yellowfin tuna		Striped marlin		Spearfish		Mahimahi	
				N (M,S)	Moving (%)	*N* (M,S)	Moving (%)	*N* (M,S)	Moving (%)	*N* (M,S)	Moving (%)	*N* (M,S)	Moving (%)
40–80	1989	546	489	1 (0,0)	—	0 (0,0)	—	5 (0,2)	0	4 (1,1)	50	3 (0,0)	—
	1990	1214	822	0 (0,0)	—	4 (0,2)	0	16 (1,5)	17	8 (0,7)	0	41 (5,14)	26
80–120	1989	684	586	0 (0,0)	—	1 (0,1)	0	9 (1,3)	25	4 (1,1)	50	2 (0,1)	0
	1990	1612	1026	2 (0,1)	0	0 (0,0)	—	15 (2,7)	22	5 (0,4)	0	14 (1,7)	12
120–160	1989	658	558	2 (0,2)	0	0 (0,0)	—	6 (2,1)	25	5 (1,3)	25	1 (0,0)	—
	1990	1611	1007	0 (0,0)	—	3 (0,2)	0	3 (1,1)	50	3 (0,2)	0	5 (1,3)	25
160–200	1989	350	281	1 (0,1)	0	0 (0,0)	—	2 (1,1)	50	1 (1,0)	100	0 (0,0)	—
	1990	1812	1151	6 (1,2)	33	4 (0,1)	0	5 (1,0)	100	5 (0,1)	0	6 (0,1)	0
200–240	1989	553	427	6 (1,3)	25	1 (1,0)	100	2 (0,0)	—	1 (0,1)	0	1 (1,0)	100
	1990	1160	748	11 (1,6)	14	1 (0,0)	—	1 (0,1)	0	0 (0,0)	—	4 (0,0)	—
240–280	1989	524	406	5 (0,3)	0	1 (0,1)	0	0 (0,0)	—	0 (0,0)	—	1 (0,0)	—
	1990	1321	795	11 (0,6)	0	1 (0,0)	—	0 (0,0)	—	0 (0,0)	—	6 (1,0)	100
280–320	1989	353	279	3 (0,1)	0	0 (0,0)	—	0 (0,0)	—	1 (0,1)	0	1 (0,0)	—
	1990	626	395	7 (0,4)	0	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—	1 (0,0)	—
320–360	1989	384	288	7 (1,4)	20	0 (0,0)	—	2 (1,0)	100	4 (2,1)	67	0 (0,0)	—
	1990	198	152	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—
360–400	1989	214	148	6 (1,3)	25	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—
	1990	108	84	2 (0,1)	0	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—	1 (0,0)	—
400+	1989	87	60	2 (0,0)	0	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—
	1990	276	225	2 (0,0)	—	0 (0,0)	—	0 (0,0)	—	0 (0,0)	—	2 (1,0)	100
Total	1989	4352	3522	33 (3,17)	15	3 (1,2)	33	26 (5,7)	38	20 (6,8)	43	9 (1,1)	50
	1990	10,058	6402	41 (2,20)	9	13 (0,5)	0	40 (5,14)	26	21 (0,14)	0	80 (9,25)	26
Combined total		14,410	9924	74 (5,37)	12	16 (1,7)	12	66 (10,21)	32	41 (6,22)	21	89 (10,26)	28

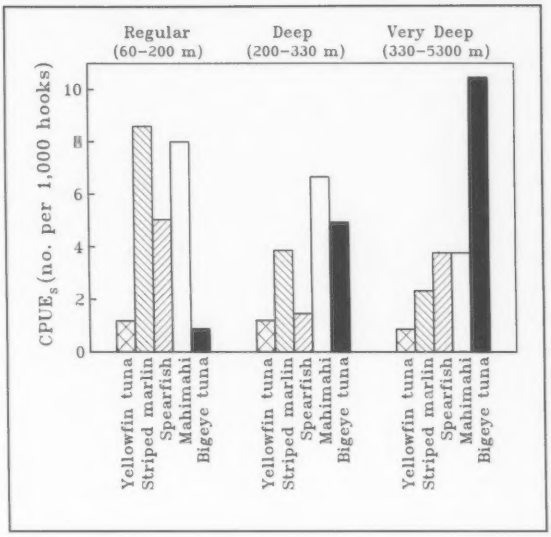


Figure 9

Comparison between indices of fish abundance from different types of longline sets, calculated as the number of fish caught/1000 hooks without regard to capture depth of individual fish ($CPUE_S$). Three types of longline sets were categorized on the basis of the deepest hooks, but every set contained some hooks as shallow as 40–80 m. Data are combined for 1989 and 1990.

Although relatively few mahimahi were captured with timer data, these data indicated maximum abundance was at 40–80 m in 1990 (only one fish was caught on a settled hook in 1989; Fig. 7, Table 4). Pooled data clearly indicated that $CPUE_D$ was highest at 40–120 m (Fig. 8). At >200 m, all mahimahi with timer data were caught on moving hooks.

Examining the $CPUE_S$ data as if the only available depth information were the set type (Fig. 9) made it difficult to correctly qualify the relative abundance of fish in relation to depth. For example, mahimahi appeared almost as abundant in deep sets as in shallow sets, and spearfish appeared more abundant in very deep than in deep sets, illustrating that it is impossible to correctly describe fish depth distributions without data on catch by hook position, hook depth, and capture time.

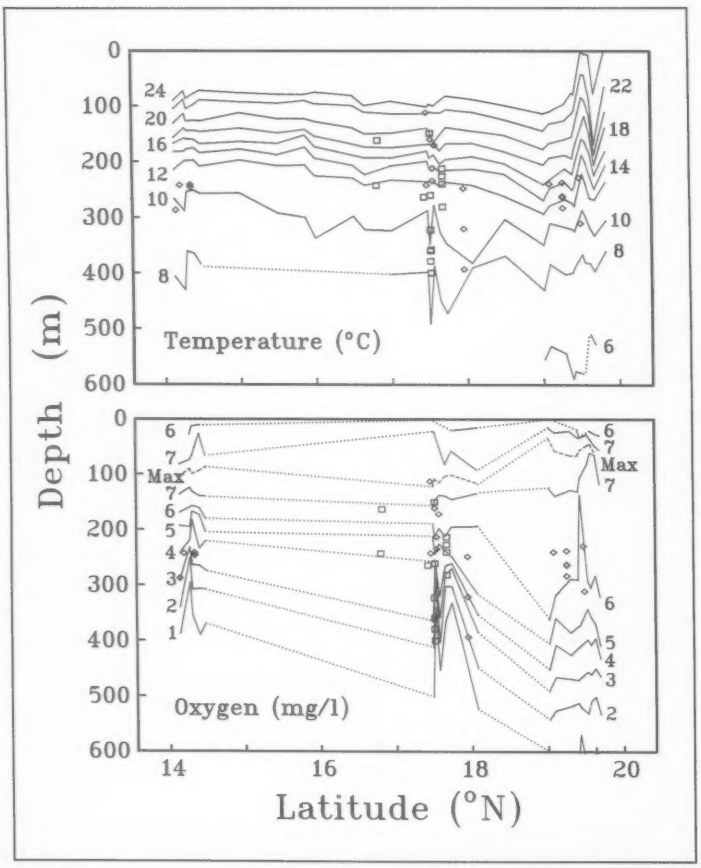


Figure 10

Temperature and dissolved oxygen profiles of the study area (lat. 14°–20°N, long. 148°–159°W) in 1990 (similar to 1989). Confirmed capture depths of bigeye tuna in 1989 (□) and 1990 (◇) are indicated.

Oceanographic habitat

The temperature profile in 1990 (Fig. 10) was representative of the study area in both years, except the bottom of the thermocline (i.e., the 12°C isotherm) was ~40 m deeper in 1989. In both years, the highest catch rate of bigeye tuna with confirmed capture depths occurred at lat. 17°–18°N at 360–400 m in temperatures of 8°–10°C (Fig. 10).

The oxycline in 1990 (Fig. 10) also was similar to that in the previous year (i.e., the 3.0 mg/L isopleth was only 10–20 m deeper in 1989). Most bigeye tuna were caught at DO concentrations of 2–6 mg/L. In both years, the highest catch rate was at 2–3 mg/L.

Table 5

Standardized distribution of hooks by depth stratum for four standardized gear types and predicted catch-per-unit-effort (CPUE) for each gear type based on the weighted average observed CPUE by hook depth for five commercially-important species in research longline sets off Hawaii, 1989 and 1990. For each species, relative gear efficiency is given as the ratio between the CPUE for each gear type and for regular gear (too few yellowfin tuna (N 3) were caught in 1989 to warrant calculating relative gear efficiency).

Model gear type	Hook number by depth (m)								Bigeye tuna		Yellowfin tuna		Striped marlin		Shortbill spearfish		Mahimahi	
	40–80	80–120	120–160	160–200	200–240	240–280	280–320	Year	CPUE	CPUE ratio	CPUE	CPUE ratio	CPUE	CPUE ratio	CPUE	CPUE ratio	CPUE	CPUE ratio
Regular	0	2	2	2	0	0	0	1989	1.93	1.00	0.47		9.30	1.00	5.37	1.00	1.43	1.00
								1990	1.52	1.00	1.36	1.00	4.83	1.00	2.57	1.00	5.03	1.00
								$\bar{x}$	1.73	1.00	0.91		7.07	1.00	3.97	1.00	3.23	1.00
Deep	0	2	2	2	2	2	3	1989	5.95	3.08	0.78		4.85	0.52	3.50	0.65	1.88	1.31
								1990	6.02	3.97	0.88	0.65	2.36	0.49	1.19	0.46	4.45	0.88
								$\bar{x}$	5.99	3.53	0.83		3.60	0.51	2.34	0.56	3.16	1.10
Shallow	2	2	2	0	0	0	0	1989	1.60	0.83	0.47		10.43	1.12	6.83	1.03	3.23	2.26
								1990	0.41	0.27	1.72	1.27	8.12	1.68	3.85	1.50	15.18	3.02
								$\bar{x}$	1.01	0.55	1.09		9.28	1.40	5.34	1.39	9.21	2.64
New	0	0	0	2	2	2	3	1989	7.93	4.10	0.82		2.04	0.22	2.09	0.39	1.76	1.22
								1990	8.42	5.55	0.85	0.63	0.93	0.19	0.61	0.24	3.81	0.76
								$\bar{x}$	8.18	4.82	0.84		1.49	0.20	1.35	0.32	2.78	0.99

The area (lat. 17°–18°N) of highest catch rates for bigeye tuna was on the south edge of a northward transition to a deeper thermocline and oxycline (Fig. 10). The north-south pattern is typical of the central Pacific Ocean at these latitudes, whereas the highly variable pattern in the thermocline between lat. 19.4° and 20°N was probably caused by the proximity to the lee side of the island of Hawaii.

With regard to the other species, the thermal structure of the habitat (Fig. 10) and the confirmed depth distribution of fish (Figs. 4, 7, and 8) suggested that yellowfin tuna were most abundant in the mixed layer (24°–25°C) and the steepest part of the thermocline down to about 15°C. Striped marlin appeared to be most abundant in the mixed layer and the top of the thermocline to ~20°C. Spearfish appeared to occupy a habitat between that of yellowfin tuna and striped marlin, and mahimahi occupied the mixed layer.

Standardized gear efficiency

For bigeye tuna in 1989–90, the CPUE ranges for standardized deep gear and proposed new gear were about 3.1–4.0 and 4.1–5.6 times, respectively, as great as those for regular gear (Table 5). Shallow gear on average was about half as efficient as regular gear in catching bigeye tuna, whereas it was about 40% more efficient than regular gear in catching spearfish and striped marlin. Deep gear was only about half as efficient as regular gear in catching striped marlin and spearfish, and the proposed new gear was only about 20% as efficient for striped marlin and about 30% as efficient for spearfish.

The numbers of yellowfin tuna and mahimahi caught in 1989 were much lower than in 1990, so the latter year provided better data for calculating gear efficiency for these species (Table 5). Shallow gear was about 3.0 times as efficient at catching mahimahi, and deep and new gear reduced efficiency to about 90% and 75% in comparison with regular gear. For yellowfin tuna, shallow gear was about 25% more efficient than regular gear, whereas the deep and new gear types were each about 65% as efficient.

Discussion

Habitat depth

Hook timers are useful in confirming whether fish are caught while longline hooks are sinking, settled, or rising. Combined with capture depths from TDRs, hook timers offer a new method for establishing the habitat depth of large pelagic fishes. Stock assessments (Suzuki 1989) depend on the estimation of effective effort, defined as fishing effort corrected for differences in efficiency due to gear and habitat depth (Suzuki et al. 1977). Improving the definition of tuna and billfish habitats and the estimation of effective effort in those habitats should lead to significant improvements in assessing true abundance.

Comparisons of CPUE by two gear types provide only qualitative information on habitat depth. For

example, since deep gear is more efficient than regular gear for bigeye tuna, this species must occupy a relatively deep habitat (Suzuki et al. 1977). More specific information on habitat depth is provided by catches and $CPUE_H$ by hook position (Hanamoto 1979 and 1987, Hanamoto et al. 1982, Suzuki and Kume 1982), especially when TDRs are used to record gear depth (Saito 1973 and 1975, Hanamoto 1974, Nishi 1990). Capture depth estimates without TDR records ignore major variations in actual gear depth (Fig. 2; Nishi 1990), and those without hook timers are biased by the inclusion of inappropriate hook depths.

A possible source of bias in the present study is the inclusion of some falsely confirmed depths due to fish being caught with timers already activated. The proportion of false estimates should be similar to the frequency of timers that were without fish and were triggered while settled, which was only 3.9% in 1989 and 2.6% in 1990 (Table 3). Thus it is unlikely that >4% of confirmed capture depths in this study are incorrect because of false timer readings.

Many pelagic longline studies (Saito 1975, Hanamoto 1976, Yang and Gong 1988) assume that fish are caught while hooks are at settled depths. Supporting this assumption, Saito (1973) has shown that albacore *Thunnus alalunga* are caught almost exclusively by settled hooks, based on capture times indicated by fluctuations in TDR records. Using hook timers, the present study adds new information: Almost 90% of bigeye and yellowfin tuna also are caught while hooks are at settled depths (Table 4). However, hook timers indicate this generalization does not extend to striped marlin, spearfish, mahimahi (Table 4), and most of the commercially unimportant species (Fig. 5). Although most of these fish are also caught on settled hooks, a substantial fraction are not, and this must be considered when quantifying their depth ranges (Fig. 4).

Besides the present study, little information exists on longline capture depths for mahimahi, spearfish, and striped marlin. In the study area, $CPUE_D$ values for these species (Fig. 7) indicate maximum abundance at depths in the mixed layer for mahimahi (<100 m, 24°–25°C; Fig. 10), extending into the top of the thermocline for striped marlin (120 m, 20°C) and into the middle of the thermocline for spearfish. Striped marlin are reported to be caught most frequently on longline hooks closest to the surface (60–90 m) in the eastern tropical Pacific and Indian Oceans, but they may be more abundant above this depth (Hanamoto 1979, Hanamoto et al. 1982). Mahimahi and spearfish may also be more abundant above the uppermost stratum (40–80 m) in the present study, since their catch rates appear to increase towards the surface (Fig. 7).

Striped marlin are also reported caught on deep longline hooks (~200 m; Hanamoto et al. 1982) and at the deep end of vertical longline gear (336 m; Saito 1973); but in the present study, their deepest confirmed capture depth is 210 m. Tracking data on striped marlin off California indicate a shallow (<60 m) depth distribution with most of the daytime spent within 10 m of the surface (Holts and Bedford 1989).

The depth distribution (200–400 m) of bigeye tuna in the present study is deeper than in many previous reports (Hanamoto 1974, 50–160 m; Saito 1975, 207–245 m; Suzuki and Kume 1982, 170–300 m; Yang and Gong 1988, 260–300 m; Nishi 1990, 140–180 m), although these studies have found bigeye tuna are most abundant on the deepest hooks fished. Hanamoto (1987) hypothesizes a habitat depth of 250–400 m for the central Pacific Ocean at latitude 25°N, based on the observed maximum longline CPUE at temperatures of 10°–15°C. The highest $CPUE_D$ values in the present study are at the cold, deep end of this range (Fig. 7), deeper than most hooks used in commercial fishing gear. However, the $CPUE_D$ value at 280–400 m is not significantly different from that at 200–400 m (Fig. 8). Although these results may be specific to January and February, perhaps commercial CPUE could be improved by increasing fishing depth, at least during winter months.

Seasonal and geographic variation in temperature and DO profiles may affect the depth preferences of pelagic fish. Hanamoto (1975, 1987) has hypothesized that the deep end of bigeye tuna habitat is limited by DO concentrations below 1 mL/L (1.4 mg/L) and by temperatures below 10°C. Results of the present study suggest that bigeye tuna are seldom caught in waters with a DO concentration of ~<2 mg/L (Fig. 10). Oxygen concentrations of ~2–3 mg/L cause significant reductions in bigeye tuna cardiac output (1.9–2.6 mg/L) and heart rate (2.7–3.5 mg/L), suggesting that bigeye tuna cannot maintain a full range of activity at lower DO concentrations (Bushnell et al. 1990).

Longline data to support the hypothesis of a 10°C temperature limit independent of the DO limit are sparse. Few hooks have been deployed in waters colder than 9°–10°C with DO concentrations of >1 mL/L (Hanamoto 1975, 1987). In the present study, the only area with DO values >2 mg/L and temperatures <8°C was at lat. 10°–20°N (Fig. 10). Currents prevented hooks from reaching cold (6°–8°C) water in this area.

Sonic tracking of bigeye tuna around Hawaii indicates a depth distribution slightly shallower than that in longline studies (Hanamoto 1987, 250–400 m; present study, 200–400 m). Holland et al. (1990) have reported that tracked bigeye tuna spend most of the daytime at 200–240 m in 14°–17°C water. This may be due to the association of the tracked bigeye tuna with fish aggregating devices or due to a size-related difference. The 72- to 74 cm bigeye tuna studied by Holland

et al. (1990) weighed ~10–12 kg, whereas longline-caught bigeye tuna in the present study averaged >30 kg.

Results of the present study apply predominantly to daytime habitat depths, but an important difference apparently exists between the daytime and nighttime depth distributions of bigeye tuna (Holland et al. 1990). At night, tracked bigeye tuna move upward to ~70–90 m at temperatures of 23°–25°C. Confirmation of this nocturnal behavior comes from a new nighttime longline swordfish fishery that has recently developed in Hawaii using chemical light sticks. Although this fishery deploys very shallow (generally <90 m) gear, the bycatch of bigeye tuna is surprisingly high (S. Pooley, NMFS Honolulu Lab., pers. commun., April 1991), indicating that bigeye tuna have a shallow nighttime depth distribution.

The small number of yellowfin tuna caught in this study makes estimated habitat depth (40–200 m) less certain, but it does not differ much from the 90–230 m depth found in Suzuki and Kume (1982) and Yang and Gong (1988). Tracking studies (Carey and Olson 1982, Holland et al. 1990) show yellowfin tuna spend most of their time at depths <100 m. Depths of the highest longline $CPUE_D$ for yellowfin tuna in the present study (40–80 m; Fig. 7) are similar to the depths (30–80 m) at which tracked yellowfin tuna in Hawaii spend over 50% of their time during the day (Holland et al. 1990), tending to confirm that yellowfin tuna habitat is mostly in the mixed layer.

Methods for estimating habitat depths in the present study could be improved by increasing the number of TDRs deployed or by developing a model, calibrated with TDRs, to predict gear depth based on wind and current measurements, divergence or convergence of floats, and stops and starts in deployment and retrieval. Procedures to estimate the capture depths of fish caught while hooks are sinking or rising could also be developed, but would depend on very accurate timekeeping, since the gear rises rapidly during retrieval (Fig. 3).

Catch by moving hooks

The catch of shallow-swimming species on deep hooks moving through shallower depths could reduce the selectivity of gear designed to catch deep-swimming species. The results show that moving longline hooks are more effective (per unit time) than settled hooks at catching billfish, mahimahi, some sharks, and most other non-tuna species. However, the majority of these fish are caught on settled hooks, because of the longer time that hooks are settled (Fig. 5). The relative amount of time hooks are moving vs. settled is the only aspect of the commercial daytime tuna longline operations that differs much from the fishing method used in this study. The gear is left in the water longer and then retrieved more rapidly during commercial fishing, so hooks spend less time moving and more time settled. This may result in greater proportions of fish being caught on settled hooks by commercial fishermen than in the present study.

Eliminating shallow-settled hooks should greatly reduce the catch of shallow-swimming species. For non-tuna species, deploying and retrieving the gear less often (as in commercial operations) should decrease the CPUT (catch-per-unit-time), but would increase the CPUE because the latter increases with set duration. In contrast, bigeye tuna CPUT and CPUE should increase with less frequent deployment and retrieval, because CPUT is highest for settled hooks.

The mechanism for increased CPUT on moving hooks for non-tuna species is unclear. Moving bait may be more attractive than settled bait, but the low number caught on sinking hooks (Fig. 5) suggests that gear motion alone is not responsible for increased catch rate. Perhaps a gradual aggregation of fish around the gear (or the vessel) while the gear is settled contributes to the catch rate by rising hooks.

Although hook timer data provide a reliable way to confirm when fish are caught on settled hooks, such data may be less reliable as a measure of fish caught on moving hooks, because of the uncertainty regarding fish with timers triggered at recovery (Fig. 5). These fish are not included in the number captured on moving hooks (Table 4); their timer readings cannot be distinguished from ones triggered after being brought aboard. Therefore, the estimates of fish caught on moving hooks (Table 4) may be too low. Alternatively, if these readings indicate a tendency for some fish to not activate timers until they struggle during recovery, then the estimates of fish caught on moving hooks may be too high. In either case, only inferences regarding CPUT on moving and non-moving hooks, and the estimated proportions of fish caught on moving hooks, are affected by this uncertainty. The estimates of catches on non-moving hooks are conservative, and confirmed capture depths are not affected.

The higher proportion of fish caught on moving hooks in 1989 compared with 1990 (Table 4) could have been caused by moving hooks being less visible in 1990, since branch lines were more often recovered after dark (Table 1). Sets also lasted longer in 1990 (Table 1); this may have increased the relative proportion of catches on settled vs. moving hooks. The CPUT in relation to sinking, settled, and rising gear, and to the time of day, should be explored further using the techniques developed in the present study.

A TDR attached to vertical and regular rope longline gear sometimes records abrupt depth changes as a fish

is caught, making the TDR equivalent to a hook timer if it is close to a branch line that catches a fish (Saito et al. 1970, Saito 1973, Yamaguchi 1989). The records of TDRs at positions close to fish caught with hook timers in the present study were checked to see whether they indicated the time of capture, but the depth of the monofilament longline gear was much less stable (Fig. 3) than in the depth records of Saito et al. (1970), Saito (1973), and Yamaguchi (1989) using TDRs on rope gear. On monofilament longline gear, frequent depth changes resembling fish captures occur even when no fish are caught, making TDRs unreliable as substitutes for hook timers.

Viability of released fish

Before the present study, it was believed that fish would survive only a few hours after capture on longline gear (Grudinin 1989, Yamaguchi 1989) despite large pelagic species being known to survive capture and release from other types of gear (Foreman 1987, Squire 1987, Holts and Bedford 1989). Commercial longline fishermen in Hawaii speculated that much of their catch was made as hooks were sinking or rising, because most were alive or appeared long dead (F. Amtsberg, Der Fischen Co., Honolulu, HI 96822, pers. commun., March 1988). Based on TDR data from fish on regular longline gear (Yamaguchi 1989), vertical movements stop 1.0–1.5 h after capture for yellowfin tuna, 1.5–4.0 h for bigeye tuna, and ~0.5 h for spearfish and shark. This cessation of vertical movement has been interpreted as death (Yamaguchi 1989). Grudinin (1989) has reported on the diurnal periodicity of bigeye and yellowfin tuna catch rates based on the proportion recovered alive, assuming that tuna survive ≤2 h on longline gear. However, hook-timer results (Fig. 6) show that fish survive much longer than this, suggesting that vertical movement is not a reliable indicator of survival. Alternatively, the results of the present study could be specific to monofilament gear, which could have less resistance to moving through the water than does rope gear.

Clearly the high proportion of live fish (Table 2) is not primarily the result of capture during the 0.5 h rising period. The viability of longline-caught fish is indicated by their hooked longevity and the recovery of tagged fish. As a management option, non-retention of striped marlin and spearfish could reduce fishing mortality due to longline fishing. The importance of the reduction would depend on the length of the fishing operation; but in the present study, longline fishing mortality for striped marlin could have been reduced by 70% (Table 2) if all live fish had been released and had survived.

Gear efficiency and selectivity

Gear efficiency, defined as the dimensionless ratio of the CPUE of one gear type (i.e., deep gear) divided by the CPUE of the regular gear type, is the factor used to calculate effective effort by gear fishing at different depths (Suzuki et al. 1977). Total effective effort can then be used to calculate indices of relative abundance and to model stock production (Suzuki 1989). The most thorough approach thus far has been to calculate gear efficiency by area and season (Suzuki and Kume 1982). A better understanding of the variables that alter habitat depth would permit gear efficiency to be predicted as a function of environmental conditions, and help account for variation in abundance indices caused by environmental anomalies.

The relative efficiency of standardized deep gear (Table 5) follows the pattern observed in previous studies (Suzuki et al. 1977, Yang and Gong 1988) in which deep gear is more efficient at catching bigeye tuna and less efficient at catching yellowfin tuna and istiophorid billfish. However, the estimated efficiency of the standardized deep gear for bigeye tuna in the present study is greater (ratio 3.1–4.0 over the 2 years; Table 5) than that reported by Suzuki et al. (1977) for the central and western equatorial Pacific (1.8) or by Yang and Gong (1988) for the Atlantic (1.9). Suzuki and Kume (1982) have presented graphs of deep and regular CPUE for bigeye tuna on a quarterly basis by area throughout the Pacific, and these data indicate very little difference between gear types in the central Pacific north of lat. 15°N. The high efficiency estimated for deep gear in the present study may partly result from using measured depths rather than inferred depths to define deep and regular gear types. Also, a high relative efficiency for deep gear may be specific to the Hawaii area in the winter season.

The relative efficiency of deep gear for yellowfin tuna in the Atlantic (0.95, Yang and Gong 1988) is greater than in the central and western equatorial Pacific (0.73, Suzuki et al. 1977) and in the present study (0.65, Table 5). Relative efficiency of deep gear for striped marlin in the central and western equatorial Pacific (0.28, Suzuki et al. 1977) is much lower than in the central Pacific north of Hawaii (0.74, Suzuki 1989), nicely bracketing the estimate from the present study (0.51, Table 5).

The model estimates of gear efficiency (Table 5) are not meant to supplant earlier estimates based on much larger data sets (Suzuki et al. 1977, Suzuki and Kume 1982, Yang and Gong 1988, Suzuki 1989), but rather to show how catch by hook position can be used to estimate CPUE by different gear configurations, especially hypothetical configurations for which no real data exist. Efficiency estimates (Table 5) suggest that

shallow sets of the type hypothesized to represent early use of monofilament longline gear in Hawaii would be expected to catch about 40% more billfish and 160% more mahimahi than would regular longline gear. Large increases in longline catches of these fish in Hawaii have occurred in recent years (1989–90, Boggs 1991) as the expanding Hawaii fishery adopted a new type of gear. The proposed new gear configuration would be an effective way to reduce the catch of spearfish and striped marlin by ~70–80% below that of regular gear.

Hook timers and TDRs are useful in documenting the depth distribution and habitat of pelagic fish and in showing how different configurations of longline gear and the release of live fish can be effective means of reducing fishing mortality for some species. Better methods of identifying the habitats of pelagic fishes should make it easier to estimate real changes in fish abundance by accounting for changes in fishing methods and the environment.

Acknowledgments

Several of Hawaii's longline fishermen, especially F. Amtsberg, provided technical advice without which few fish would have been caught. Many of the staff at the Honolulu Laboratory participated in the cruises, and their creativity and hard work contributed substantially to this study, especially R.K.C. Chang, A.E. Chun, R. Ito, L.A. Koch, R.A. Skillman, D. Therry, J.H. Uchiyama, and S. Yano. L.A. Koch tabulated the data and produced the figures, and B.S. Kikkawa provided invaluable help in acquiring and manufacturing the hook timers. Volunteer assistance on the research cruises was given by H. Dewer, P. Fields, C. Hayashi, and A. Sesawa. The officers and crew of the NOAA ship *Townsend Cromwell* also were very helpful, especially LT R. Brainard, LTC B. Dearbaugh, H. Lariosa, and CDR R. Marriner.

Citations

Boggs, C.H.
1990 Longline research on tuna and marlin. *In* Relatorio, X Semana das Pescas dos Acores, March 12–16 1990, p. 249–252. Sec. Reg. Agric. Pescas, Dir. Reg. Pescas, Horta, Faial, Azores.
1991 A preliminary examination of catch rates in Hawaii's troll and handline fisheries over a period of domestic longline fishery expansion. Admin. Rep. H-91-05, NMFS Southwest Fish. Sci. Cent., Honolulu, 62 p.

Bushnell, P.G., R.W. Brill, and R.E. Bourke
1990 Cardiorespiratory responses of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) to acute reductions of ambient oxygen. Can. J. Zool. 68:1857–1865.

Carey, F.G., and R.J. Olson
1982 Sonic tracking experiments with tunas. Int. Comm. Conserv. Atl. Tunas Collect. Vol. Sci. Pap. 17:458–466.

Foreman, T.J.
1987 A method of simultaneously tagging large oceanic fish and injecting them with tetracycline. Fish. Bull., U.S. 85: 645–647.

Grudinin, V.B.
1989 On the ecology of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*). J. Ichthyol. 26(6):22–29.

Hanamoto, E.
1974 Fishery oceanography of bigeye tuna—I. Depth of capture by tuna longline gear in the eastern tropical Pacific Ocean. La Mer (Bull. Soc. Franco-Japonaise Oceanogr.) 12(3):128–136.
1975 Fishery oceanography of bigeye tuna—II. Thermocline and dissolved oxygen content in relation to tuna longline fishing grounds in the eastern tropical Pacific Ocean. La Mer (Bull. Soc. Franco-Japonaise Oceanogr.) 13(2):58–71.
1976 The swimming layer of bigeye tuna. Bull. Jpn. Soc. Fish. Oceanogr. 29:41-44. [Engl. transl. no. 21 by Tamio Otsu, 1977, 7 p.; avail. NMFS Honolulu Lab., Honolulu 96822-2396.]
1979 Fishery oceanography of striped marlin—IV swimming layer in the tuna longline fishing grounds. Bull. Jpn. Soc. Sci. Fish. 45:687–690.
1987 Effect of oceanographic environment on bigeye tuna distribution. Bull. Jpn. Soc. Fish. Oceanogr. 51:203–216.

Hanamoto, E., T. Shibata, and H. Okui
1982 Some considerations on the vertical distribution particularly of the striped marlin in the Indian Ocean and on the fishing characteristics of the tuna longline gear. Kanagawa Prefect. Fish. Exp. Stn. Res. Rep. 4:17–21.

Holland, K.N., R.W. Brill, and R.K.C. Chang
1990 Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. Fish Bull., U.S. 88:493–507.

Holts, D., and D. Bedford
1989 Activity patterns of striped marlin in the Southern California Bight. *In* Stroud, R.H. (ed.), Planning the future of billfishes, research and management in the 90's and beyond. Part 2: Contributed papers. Mar. Rec. Fish. 13: 81–93. Natl. Coalition Mar. Conserv., Savannah, GA.

Kawamoto, K.E., R.Y. Ito, R.P. Clarke, and A.E. Chun
1989 Status of the tuna longline fishery in Hawaii, 1987–1988. Admin. Rep. H-89-10, NMFS Southwest Fish. Sci. Cent., Honolulu, 34 p.

Nishi, T.
1990 The hourly variations of the depth of hooks and the hooking depth of yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*), of tuna longline in the eastern region of the Indian ocean. Mem. Fac. Fish. Kagoshima Univ. 39: 81–98.

Rockefeller, W.
1989 Looking to the future of billfishes. *In* Stroud, R.H. (ed.), Planning the future of billfishes, research and management in the 90's and beyond. Part 1: Fishery and stock synopses, data needs and management. Mar. Rec. Fish. 13:11–14. Natl. Coalition Mar. Conserv., Savannah, GA.

Saito, S.
1973 Studies on fishing of albacore, *Thunnus alalunga* (Bonnaterre) by experimental deep-sea tuna long-line. Mem. Fac. Fish. Hokkaido Univ. 21:107–185.
1975 On the depth of capture of bigeye tuna by further improved vertical long-line in the tropical Pacific. Bull. Jpn. Soc. Sci. Fish. 41:831–841.

Saito, S., K. Ishii, and K. Yoneta
1970 Swimming depths of large sized albacore in the South Pacific Ocean — 1. Fishing of albacore by a newly designed vertical longline. Bull. Jpn. Soc. Sci. Fish. 36:578–584.

Somerton, D.A., B.S. Kikkawa, and C.D. Wilson
1988 Hook timers to measure the capture time of individual fish. Mar. Fish. Rev. 50(2):1–5.

Squire, J.L.
1987 Striped marlin, *Tetraptuturs audax*, migration patterns and rates in the northeast Pacific Ocean as determined by a cooperative tagging program: Its relation to resource management. Mar. Fish. Rev. 49(2):26–43.

Squire, J.L., and D.W.K. Au
1990 Striped marlin in the northeast Pacific—a case for local depletion and core area management. *In* Stroud, R.H. (ed.), Planning the future of billfishes, research and management in the 90's and beyond. Part 2: Contributed papers. Mar. Rec. Fish. 13:199–214. Natl. Coalition Mar. Conserv., Savannah, GA.

Suzuki, Z.
1989 Catch and fishing effort relationships for striped marlin, blue marlin, and black marlin in the Pacific Ocean, 1952 to 1985. *In* Stroud, R.H. (ed.), Planning the future of billfishes, research and management in the 90's and beyond. Part 1: Fishery and stock synopses, data needs and management. Mar. Rec. Fish. 13:165–177. Natl Coalition Mar. Conserv., Savannah, GA.

Suzuki, Z., and S. Kume
1982 Fishing efficiency of deep longline for bigeye tuna in the Atlantic as inferred from the operation in the Pacific and Indian Oceans. Int. Comm. Conserv. Atl. Tunas Collect. Vol. Sci. Pap. 17:471–486.

Suzuki, Z., Y. Warashina, and M. Kishida
1977 The comparison of catches by regular and deep tuna longline gears in the western and central equatorial Pacific. Bull. Far Seas Fish. Res. Lab. 15:51–83.

Yamaguchi, Y.
1989 Tuna long-line fishing IV: Fish ecology in the context of tuna long-line fishing. Mar. Behav. Physiol. 15:45–73.

Yang, W.S., and Y. Gong
1988 The vertical distribution of tunas and billfishes, and fishing efficiency between Korean regular and deep longlines in the Atlantic Ocean. Bull. Natl. Fish. Res. Dev. Agency [Pusan, Korea] 42:39–42.

Yoshihara, T.
1954 Distribution of catch of tuna longline-IV. On the relation between k and $\varphi°$ with a table and diagram. Bull. Jpn. Soc. Sci. Fish. 19:1012–1014.

Reproduction in American lobsters *Homarus americanus* transplanted northward to St. Michael's Bay, Labrador

Frank A. Boothroyd

Biology Department, Memorial University of Newfoundland
St. John's, Newfoundland A1B 3X9, Canada

Gerald P. Ennis*

Department of Fisheries and Oceans, P.O. Box 5667
St. John's, Newfoundland A1C 5X1, Canada

Abstract. – In the summers of 1982, 1983, and 1985, almost 5000 commercial lobsters were transplanted from an area on the northeast coast of Newfoundland to St. Michael's Bay in southern Labrador, about 200 km beyond their reported northern limit of distribution, in an attempt to establish a self-sustaining population. Biological sampling of these lobsters was carried out each summer from 1986 to 1991. A continuous shift to larger sizes and a generally high incidence of new-shell animals indicated molting was a common occurrence in these lobsters. All nonovigerous females had ovaries developing for extrusion that summer, and their seminal receptacles were full. In contrast, percentages of ovigerous females were low and most of these had extruded recently. Many ripe females apparently failed to extrude, and many that did extrude lost the entire clutch before the following summer. Exposure to temperatures near or below 0°C from mid-November to mid-May, and to near-continuous darkness below a layer of ice during most of this period, may cause a high incidence of resorption of ripe ovaries. The incidence of ovigerous females with recently-extruded eggs increased substantially in the later years of the study, indicating a degree of physiological adjustment to the adverse environmental conditions. However, loss of the entire clutch of eggs continued to be prevalent. Prolonged low temperature certainly retarded embryonic development for the females that extruded and retained their eggs. Six of 17 ovigerous females with old, eyed eggs had less than half the yolk remaining. Only one brood would have hatched by early August, long enough in advance of autumn cooling for development to Stage IV and settlement in the area to be possible. Lobsters transplanted to St. Michael's Bay will not likely become a self-sustaining population. Any recruitment that might occur would certainly be too little and too irregular to support a fishery.

Manuscript accepted 15 July 1992.
Fishery Bulletin, U.S. 90:659–667 (1992).

The American lobster *Homarus americanus* occurs in the western Atlantic Ocean from the Strait of Belle Isle area of southern Labrador and the northern tip of the island of Newfoundland south to North Carolina (Cooper and Uzmann 1980). The species supports commercial fisheries of considerable economic importance throughout most of its range. Its high commercial value led to repeated attempts to establish lobster populations on the Pacific coast of North America, but none of the transplants was successful (Conan 1986). In recent years, the Provincial Government of Newfoundland and Labrador transplanted commercial (mostly adult) lobsters from an area on the northeast coast of the island of Newfoundland to a location ~200 km beyond the reported northern limit of distribution in St. Michael's Bay, Labrador (Fig. 1). The bay extends inland ~28 km from the open coast and contains numerous small islands, features promoting a circulation pattern that would aid retention and eventual settlement in the area of any larvae produced by the transplanted lobsters. This was an important consideration, since the aim of the transplant was to establish a self-sustaining population that would eventually support a fishery.

Lobsters were transplanted to St. Michael's Bay in the summers of 1982, 1983, and 1985. Biological sampling was conducted each summer from 1986 to 1991. Our purpose is to present observations related to various aspects of population biology, in particular, molting, mating, ovary development, spawning and embryonic development, and consider the possibility of this transplanted population being or becoming self-sustaining.

Methods and materials

Lobsters transplanted to St. Michael's Bay were caught during May–June by commercial fishermen near Comfort Cove, Notre Dame Bay, on the northeast coast of Newfoundland (Fig. 1). They were purchased from a local buyer by the Newfoundland and Labrador Department of Fisheries and transported directly to St. Michael's Bay by float plane. Transplants were made in 1982, 1983, and 1985 and totaled 2174 males, 81–114 mm carapace length (CL), and 2310 nonovigerous females, 81–112 mm CL. Lobsters were released once only at eight widely-separated sites around the bay where the shallow-water habitat appeared quite suitable for lobsters.

The authors conducted biological sampling annually in the summer-

* Reprint requests should be addressed to this author.

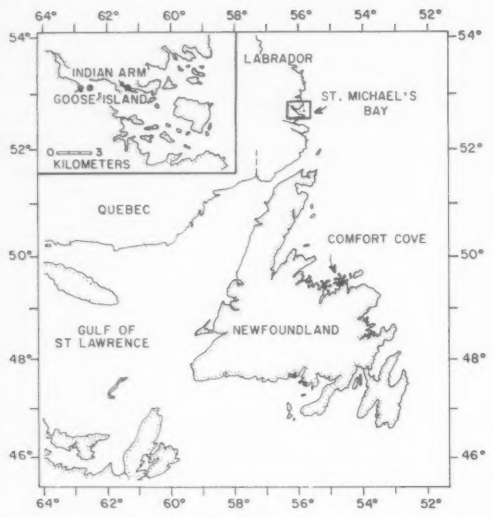


Figure 1

Locations of Comfort Cove, Newfoundland, and St. Michael's Bay, Labrador, the donor and recipient sites, respectively, for lobsters *Homarus americanus* transplanted to Labrador. Insert shows Goose I. and Indian Arm, the main sites in St. Michael's Bay where transplanted lobsters were sampled.

time from 1986 to 1990. In 1991, less detailed sampling was carried out by the Department of Fisheries of the Province of Newfoundland and Labrador. Sampling focused on lobsters in Indian Arm (transplanted in 1982) and at Goose Island (transplanted in 1985) (Fig. 1). These two sites were selected to include lobsters from the earliest and latest transplants. Also, in initial trap sampling in 1986, lobsters were caught more readily at these sites than at others. Lobsters were caught in baited traps in 1986, 1987, and 1991 and by scuba-diving from 1988 to 1990. Samples over the 6 years totaled 295 males and 392 females. Numbers included in sampling for various purposes described below are summarized by year and sampling site in Table 1. Carapace length of each lobster was measured to the nearest mm. Shell condition was determined by external macroscopic examination in 1986 and 1988–90. In over 90% of the lobsters examined for shell condition, those that molted the previous summer (new shell) could be readily distinguished from those that did not (old shell) by general brightness of coloration, sharpness of spines, and the degree of darkening due to abrasion on the leading edges and undersides of the claws. The others could be categorized with reasonable confidence. Each summer from 1987 to 1990, subsamples of nonovigerous females totaling 111 for the 4 years were sacrificed. For each of these, ovary color, ova diameter, contents of seminal receptacles,

Table 1

Summary of numbers included in sampling of lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985), 1986–91.

Year sampled	Number and carapace lengths		Shell condition		Setal development		Nonovigerous females			Ovigerous females			
	Male	Female	Male	Female	Male	Female	Ovaries	Seminal receptacles	Cement glands	New eggs	Old eggs	Egg counts	Yolk content of old eggs
Indian Arm													
1986	87	109	87	74	—	—	—	—	—	—	21*	—	—
1987	10	25	—	—	—	—	7	7	7	1	1	2	1
1988	32	48	32	42	—	—	27	27	27	5	2	7	2
1989	24	21	24	21	24	20	8	8	8	7	6	—	6
1990	17	22	17	22	17	21	8	8	8	11	3	—	3
1991	4	9	—	—	—	—	—	—	—	4	3	—	3
Goose Island													
1986	30	32	30	30	—	—	—	—	—	0	0	—	—
1987	7	33	—	—	—	—	23	23	23	0	0	—	—
1988	16	38	10	25	—	—	7	7	7	0	0	—	—
1989	29	20	29	20	29	20	15	15	16	2	2	—	2
1990	23	22	23	22	23	22	15	15	15	7	0	—	—
1991	15	13	—	—	—	—	—	—	—	10	0	—	—

*In 1986, old- and new-egg ovigerous females were not distinguished.

and the extent of pleopod cement gland development (Aiken and Waddy 1982) were determined. In 1989 and 1990, pleopod setal development (Aiken 1973) was determined for 47 nonovigerous females and 93 males. Eighty-four ovigerous females were included among the 392 females sampled over the 6 years. Egg numbers were determined for nine collected in Indian Arm in 1987 and 1988. Five of these were small egg masses that were counted directly, the other four were estimated by drying and weighing the entire mass, then weighing and counting a subsample representing about 10% of the total. Yolk content of eggs (to the nearest tenth, i.e., 0.1) was determined for 17 ovigerous females carrying old, eyed eggs collected from 1986 to 1991. Perkins Eye Indices (PEI), which provide a measure of embryonic development (Perkins 1972), were determined for four of the latter.

From July 1986 to September 1988, a continuously recording thermograph was maintained in St. Michael's Bay at 7m within the depth range occupied by the transplanted lobsters. Mean daily temperature was obtained from the tapes. These were averaged for the first and second half of each month, with data for the different years combined. Temperature during most of June each year was not obtained because the recording tape expired in 1987 and the instrument malfunctioned in 1988. The June portion of the annual temperature regime was approximated by extrapolating from temperatures which were rising in a near-linear fashion before and after.

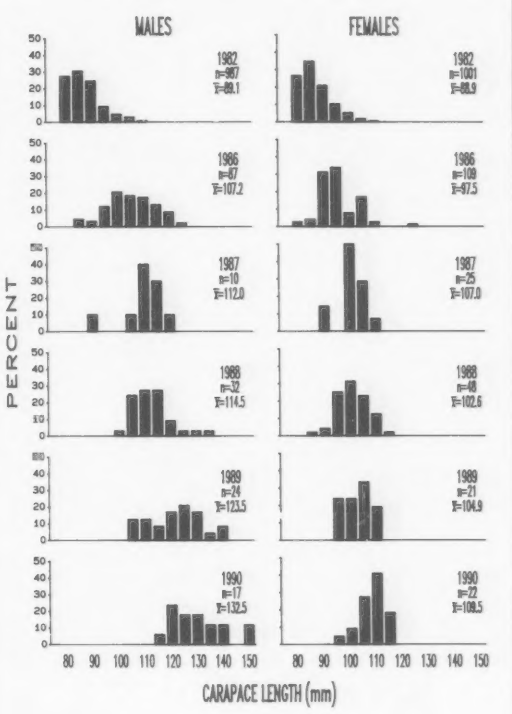


Figure 2
Size-frequencies for all male and female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador, in 1982, and when sampled at the Indian Arm release site, 1986–90.

Results

Changes in size composition

Indian Arm Mean CL of all the lobsters transplanted to St. Michael's Bay in the summer of 1982 was 89.1 mm (range 81–114mm, *N* 987) for males and 88.9mm (range 81–112mm, *N* 1001) for females (Fig. 2). We assume that these are also representative of the lobsters released at the Indian Arm site. When first sampled in the summer of 1986, mean CL of lobsters in Indian Arm had increased significantly (Tukey test; $P<0.001$) to 107.2mm for males (*N* 87) and 97.5mm for females (*N* 109). There were further shifts to larger sizes each year, especially among males, and in the summer of 1990, mean CL was significantly larger ($P<0.001$) than in all previous years at 132.5mm (range 116–153mm, *N* 17) for males and 109.6mm (range 98–116mm, *N* 22) for females.

Goose Island Mean CL of all the lobsters transplanted to St. Michael's Bay in the summer of 1985 was 84.1mm (range 81–95mm, *N* 687) for males and 84.4 mm (range 81–92mm, *N* 811) for females (Fig. 3), significantly smaller (*t*-test; $P<0.001$) than for those transplanted in 1982. We assume that these means are representative of the lobsters released at Goose I. At Goose I., annual shifts to larger sizes were small until 1988, when mean CL had increased significantly (Tukey test; $P<0.001$) to 96.4mm for males (*N* 16) and 92.6mm for females (*N* 38). By summer 1990, mean CL had increased significantly again ($P<0.001$) to 105.6mm (range 90–131mm, *N* 23) for males and to 95.9mm (range 89–105mm, *N* 22) for females.

Incidence of new-shell lobsters

The donor population at Comfort Cove is subjected to a very intensive fishery each spring which removes most of the commercial lobsters (nonovigerous and ≥81mm CL). Following the summer molting period, the vast majority of commercial-size animals in the population had molted and grown from smaller sizes

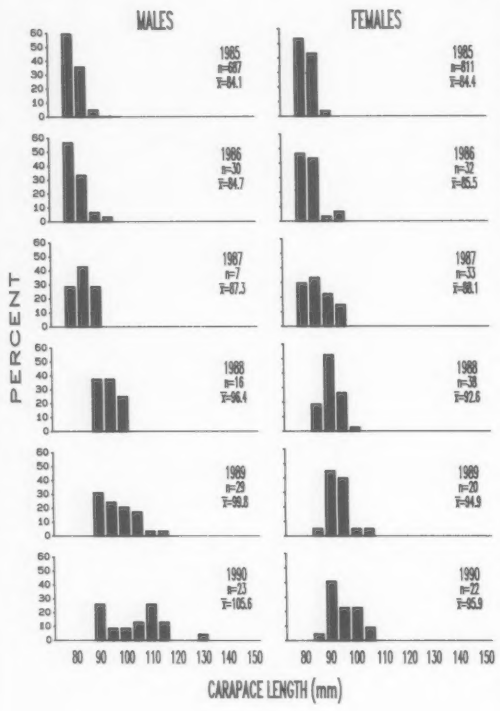


Figure 3
Size-frequencies for all male and female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador, in 1985, and when sampled at the Goose I. release site, 1986–90.

Table 2
Percentage with new shells (molted previous summer) among lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1986 and 1988–90. Number sampled in parentheses.

Year sampled	Indian Arm		Goose Island	
	Males	Females	Males	Females
1986	40.2 (87)	21.6 (74)	3.3 (30)	6.7 (30)
1988	53.1 (32)	42.9 (42)	80.0 (10)	92.0 (25)
1989	62.5 (24)	47.6 (21)	75.9 (29)	75.0 (20)
1990	52.9 (17)	31.8 (22)	52.2 (23)	63.6 (22)

Table 3
Pleopod setal development stages for male and nonovigerous female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1989–90.

Year sampled	Setal development stages* (%)					
	Males			Females		
	N	0–2.0	2.5–5.0	*N*	0–2.0	2.5–5.0
Indian Arm						
1989	24	70.8	29.2	8	62.5	37.5
1990	17	47.1	52.9	8	0	100
Goose Island						
1989	29	69.0	31.0	16	81.2	18.8
1990	23	39.1	60.9	15	0	100

* From Aiken (1973). Stages 0–2.0 indicate molting is unlikely, and stages 2.5–5.0 that molting is probable in the current summer.

during the summer. As a consequence, the incidence of new shells among commercial sizes averaged 96% and 94% for male and female lobsters, respectively, in autumn samples from 1986 to 1990 (Ennis, unpubl. data). These are much higher percentages than could be expected for the transplanted lobsters in St. Michael's Bay. There has been no lobster fishing in St. Michael's Bay and, because of their larger sizes, lobsters there are less likely to molt. Old-shell lobsters are therefore likely to be much more prevalent.

Among Indian Arm lobsters, the incidence of new shells (indicating lobsters molted the previous summer) ranged from 40.2% in 1986 to 62.5% in 1989 for males and from 21.6% in 1986 to 47.6% in 1989 for females (Table 2). In 1986, the incidence of new shells was very low among Goose I. lobsters (3.3% for males and 6.7% for females) indicating few molted in summer 1985 when they were transplanted. However, in 1988 and 1989 the incidence of new shells was quite high (75.0–92.0%) for males and females (Table 2).

Pleopod setal development was determined in 1989 and 1990 only. Percentages with advanced stages (2.5 and higher), which indicated molting would occur later in the summer, varied between years and sexes at both sampling sites. Among males, advanced stages increased from 29.2% to 52.9% and from 31.0% to 60.9% in Indian Arm and Goose I. samples, respectively, between 1989 and 1990 (Table 3). Among females, it increased from 37.5% in the Indian Arm sample and 18.8% in the Goose I. sample in 1989, to 100% in both in 1990 (Table 3).

Reproductive condition of nonovigerous females

Ovaries of 110 nonovigerous females from Indian Arm and Goose Island combined were examined from 1987 to 1990 and all were found to be medium- to dark-green

Table 4

Ovary color and ova diameter among nonovigerous female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1987–90.

Year sampled	N	Ovary color: Med. green	Ovary color: Dark green	Ova diameter (mm): $\bar{x}$	Ova diameter (mm): Range
Indian Arm					
1987–88	34	11[a]	23	1.4	0.9–1.5
1989	8	0	8[b]	1.0	0.9–1.3
1990	8	1	7	1.0	0.8–1.2
Goose Island					
1987–88	30	21[a]	9	1.3	0.9–1.5
1989	15	1	14	1.0	0.8–1.3
1990	15	0	15	1.1	0.9–1.2

[a]The high proportion with medium-green ovaries in the 1987–88 sample is probably due to a different observer than in 1989–90.
[b]Includes one specimen with yellow specks throughout the ovary, indicating resorption underway.

Table 5

Pleopod cement gland stages for nonovigerous female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1987–90.

Year	N	Cement gland stages*: 1	2	3	4
Indian Arm					
1987	7	7	0	0	0
1988	27	27	0	0	0
1989	8	7	0	1	0
1990	8	8	0	0	0
Goose Island					
1987	23	23	0	0	0
1988	7	7	0	0	0
1989	16	15	0	1	0
1990	15	15	0	0	0

*From Aiken and Waddy (1982). Stages 3 and 4 indicate extrusion will occur in the current summer.

in color, with ova 0.8–1.5 mm in diameter (Table 4). All these ovaries were developing for extrusion in the summer they were sampled; one had yellow specks characteristic of an ovary being resorbed. However, of these nonovigerous females, only 2 of 24 sampled in 1989 (2 out of 111 overall) had sufficient pleopod cement gland development (Stage 3) to indicate egg extrusion would occur (Table 5). The seminal receptacles of all of the nonovigerous females examined from 1987 to 1990 were full, which means each had mated at the last molt and was capable of fertilizing a clutch of eggs. Pleopod setal development indicated 25% of 24 and 100% of 23 nonovigerous females sampled in 1989 and 1990, respectively, would molt (Table 3). While molting does not preclude egg extrusion in the same summer, this is unlikely to occur among lobsters in St. Michael's Bay. This phenomenon probably involves only animals extruding for the first time and <81 mm CL (Ennis 1984a).

Incidence of ovigerous females

The reproductive cycle in female lobsters normally covers 2 years. Molting and mating occur one summer, egg extrusion one year later, followed by hatching of eggs, molting, and mating again in the third summer (Aiken and Waddy 1980a). Departures from this 2-year cycle known to occur in the wild include molting, mating, and extrusion in the same summer (mentioned in the preceding section) and resorption of ripe ovaries just before extrusion (Aiken and Waddy 1976 and 1980ab, Ennis 1984b). While variability in the incidence of these phenomena may contribute somewhat, the intensity of the commercial fishery and its timing in relation to the spawning season exert by far the greatest impact on the incidence of ovigerous females in a lobster population.

At Comfort Cove, most of the nonovigerous commercial-size females in the population are removed by the spring fishery just before the summer spawning period. In autumn sampling from 1986 to 1990 an average 6% of commercial-size females were ovigerous, excluding those that molted and grew from subcommercial sizes and extruded as well during the summer (Ennis, unpubl. data). Not being fished and being more likely to spawn as well because of their larger size, the percentage of females ovigerous among St. Michael's Bay lobsters by comparison should be quite high.

In St. Michael's Bay, the percentages of females that were ovigerous with old eggs each summer (i.e., extruded previous summer) were very low, particularly in 1986–88 samples, considering all nonovigerous females examined the previous summer had ripe ovaries. In the 1986 Indian Arm sample, 19.3% of the females were ovigerous, including both new- and old-egged females which were not distinguished at the time. In subsequent years, the incidence of ovigerous females with old eggs increased from 4.0% in 1987 to 33.3% in 1991 (Table 6). No ovigerous females were included in Goose I. samples until 1989, when 10% of the females carried old eggs. In 1990 and 1991 samples, however, there were none with old eggs (Table 6).

Table 6

Percentage of females that were ovigerous among lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador (Indian Arm in 1982, Goose I. in 1985) during sampling, 1986–91.

	Indian Arm				Goose Island			
Sampling dates	No. females	% new eggs	% old eggs	% ovigerous	No. females	% new eggs	% old eggs	% ovigerous
22 July–25 Aug. 1986	109	—	—	19.3*	32	0	0	0
18–25 July 26 Aug.–3 Sept. 1987	25	4.0	4.0	8.0	33	0	0	0
25 June–2 July 1988	48	10.4	4.2	14.6	38	0	0	0
19–25 July 1989	21	33.3	23.8	57.1	20	10.0	10.0	20.0
13–20 Aug. 1990	22	50.0	13.6	63.6	22	31.8	0	31.8
14–19 Aug. 1991	9	44.4	33.3	77.8	13	76.9	0	76.9

*In 1986, old- and new-egg ovigerous females were not distinguished.

The percentages of females that were ovigerous with new eggs (i.e., extruded within the preceding 2 or 3 weeks) ranged from 4% in 1987 to 50% in 1990 in the Indian Arm samples, and increased from 10% in 1989 to 32% in 1990 in the Goose I. samples (Table 6). Of 64 ovigerous females included in the combined 1987–91 samples, 73% had new eggs and, overall, there was a substantially higher incidence of ovigerous females among St. Michael's Bay lobsters in 1989–91 than previously.

The low incidence of ovigerous females in samples up to 1988 indicates most of the nonovigerous females, all of which had ripe ovaries in summer, failed to extrude eggs. In subsequent years, however, the proportion of nonovigerous females extruding increased substantially. There was no evidence of hatching of old eggs prior to our sampling each summer, which might have accounted for the scarcity of old-egged relative to new-egged females. This indicates that many females that extruded lost their entire clutch of eggs sometime prior to the following summer.

Fecundity and egg development

Egg numbers were determined for 9 ovigerous females included in the 1987 and 1988 samples from Indian Arm. Four of these egg counts were <0.1% of expected numbers as determined from a size-fecundity relationship for a population on the south coast of Newfoundland, one had 2%, and the others had 30–105% of the expected number of eggs (Table 7). The extremely low numbers in 5 of the 9 specimens cannot be attributed to high variability generally associated with such data, but rather indicate a high incidence of massive egg loss. Although egg numbers were not determined for any of 21 ovigerous females included in the 1989 and 1990 samples, cursory examination indicated that most had what appeared to be full clutches, although one had just a few hundred eggs.

Table 7

Egg numbers for nine ovigerous female lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador, included in 1987 and 1988 samples from Indian Arm.

Carapace length (mm)	No. of eggs	% of expected number*
97	15	<0.1
97	7	<0.1
101	122	<0.1
102	186	<0.1
94	334	2.0
103	6588	30.0
104	10122	45.0
102	17878	84.0
95	17854	105.0

*Expected number of eggs was calculated from a CL–fecundity relationship ($\log_{10} F = 3.0984 \log_{10} CL - 1.8963$) for a population in Placentia Bay on the south coast of Newfoundland (Ennis 1981).

The extent of embryonic development for 17 ovigerous females with old, eyed eggs collected from 1986 to 1991 ranged from 0.8 to 0.3 yolk content (Table 8). Only 6 had less than half the yolk remaining when examined. Perkins Eye Indices (PEI) were determined for four specimens. One with 0.3 yolk content had a mean PEI of 470 on 29 June 1988. At an assumed constant developmental temperature of 10°C, it was estimated, using Perkin's (1972) formula, that hatching would have occurred by 4 August. Another with 0.4 yolk content had a mean PEI of 431 on 1 August 1986, for which hatching by 21 September was estimated.

Table 8

Yolk content of eggs for 17 ovigerous females with old, eyed eggs included in 1986–91 samples of lobsters *Homarus americanus* transplanted to St. Michael's Bay, Labrador. Yolk content to the nearest tenth.

Sampling date	Carapace length (mm)	Yolk content
1 Aug. 1986	94	0.4
19 July 1987	92	0.7
29 June 1988	95	0.3
30 June 1988	97	0.8
20 July 1989	88	0.4
21 July 1989	110	0.6
21 July 1989	108	0.6
21 July 1989	103	0.7
21 July 1989	109	0.6
21 July 1989	106	0.5
22 July 1989	92	0.7
16 Aug. 1990	116	0.3
16 Aug. 1990	111	0.4
16 Aug. 1990	104	0.5
19 Aug. 1991	101	0.5
19 Aug. 1991	114	0.5
19 Aug. 1991	107	0.4

The other two PEIs were 108 and 127 (0.8 and 0.7 yolk content, respectively). Even at 10°C, well above the temperature in St. Michael's Bay beyond September, it was estimated these broods would not be ready to hatch until late December–early January.

Temperature

Bottom temperature at 7 m in St. Michael's Bay drops below 0°C in late November, remains around −1°C throughout the winter, and rises above 0°C in early June (Fig. 4). Summer warming is rapid. Temperature reaches 9°C between mid- and late-July and peaks at just over 10°C in late August. By mid-September, autumn cooling is underway and temperature starts to drop rapidly around the end of September. At Comfort Cove, where the transplanted lobsters originated, sub-zero temperatures prevail for only about 2 months in late winter (Fig. 4). Summer warming begins in late April–early May and reaches a slightly higher peak at around 11°C in late August. Autumn cooling begins somewhat later and proceeds more slowly. In St. Michael's Bay, transplanted lobsters are exposed to a similar range in temperature as at Comfort Cove, but to a substantially lower mean temperature during most of the year.

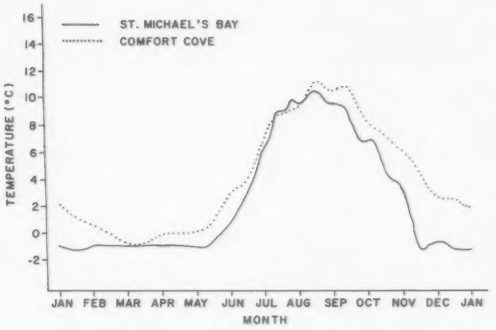


Figure 4

Annual temperature (°C) regimes from continuous-recording thermographs maintained on the bottom at 7 m in St. Michael's Bay, Labrador, summer 1986–autumn 1988, and at 9 m in Comfort Cove, Newfoundland, during the same period.

Discussion

The very low incidence of new-shell lobsters in the 1986 Goose I. sample indicates few molted in summer 1985 when they were transplanted. This was most likely due to molt inhibition caused by handling-induced stress, possibly including wide temperature fluctuations, during transplant. The high incidence of new-shell lobsters at Goose I. in 1988, and the substantial shift to larger sizes among the Indian Arm lobsters (transplanted in 1982) by 1986, indicate the transplanted lobsters acclimated over time and resumed molting despite the lower temperatures in St. Michael's Bay.

All nonovigerous females examined during the study had advanced ovaries developing for extrusion in the summer they were sampled. All of these had full seminal receptacles indicating they mated at the last molt. However, only 1.8% (2 out of 24 examined in 1989) had advanced pleopod cement gland development indicating extrusion was imminent. Some ovigerous specimens with recently-laid eggs were observed each year. This suggests most nonovigerous females that were going to extrude each summer had done so by the time our samples were collected. These amounted, however, to only 23% (N 104) of the females (excluding old-egg ovigerous) examined at Indian Arm from 1987 to 1990, and 22.5% (N 40) of those examined at Goose Island in 1989 and 1990. In 1991, this percentage increased to 66.7% (N 6) and 77% (N 13) in the Indian Arm and Goose I. samples, respectively. Advanced pleopod setal development among the ripe nonovigerous females that were examined in 1989 and 1990 indicated 62% would soon molt.

Based on the foregoing observations, it appears that up until 1990 at least most of the mature, nonovigerous females in St. Michael's Bay did not extrude. Rather, they resorbed the lipovitellin accumulated in the ripening oocytes, and many then proceeded to molt. Resorption of the ripe ovary has been associated with unfavorable holding conditions near the expected time of extrusion (Templeman 1940) but appears to be common in the wild as well (Ennis 1984b). Resorption occurs when the molting and reproductive cycles are out of phase, and molting is due to occur within 3 or 4 months after egg extrusion (Aiken and Waddy 1976, 1980ab). These cycles are normally synchronized by temperature and photoperiod regimes to ensure that when a female lobster extrudes eggs in one summer, it will not molt until after the eggs have hatched sometime the following summer.

In their experiments on the effects of winter temperature and photoperiod on spawning, Aiken and Waddy (1989) found a high incidence of resorption among mature females held at high temperature throughout the winter, particularly when a short-day photoperiod was maintained throughout the summer (55% resorbed). Onset of a long-day photoperiod in spring was necessary to trigger spawning among females held at high winter temperature. The incidence of spawning was high (≥90%) among those held at low winter temperature, even without onset of a long-day photoperiod in spring, and only a few resorbed.

These results do not explain the high incidence of resorption among female lobsters in St. Michael's Bay where they are exposed to environmental conditions well outside the foregoing experimental treatments. From mid-November to mid-May, the bottom temperature is near or below 0°C and the bay is frozen over for most of this period. Visual acuity of lobsters at very low light intensity has not been described. It seems unlikely, however, that sufficient light would penetrate a layer of snow-covered sea ice underlaid by low-salinity water (from continuous river discharge and slow mixing under the ice) for lobsters to detect a light:dark cycle. This combination of very low temperature and near continuous darkness for 5–6 months from late autumn to spring is probably the main cause of the high incidence of ovary resorption that has prevailed among female lobsters in St. Michael's Bay.

Most of the ovigerous females collected in St. Michael's Bay had extruded quite recently. The remainder were old-egged females that spawned the previous summer. Apparently, many females that extruded lost the entire clutch of eggs before the following summer. Massive but incomplete loss of eggs was also observed. Of 9 ovigerous females collected in Indian Arm in 1987 and 1988, 5 had numbers of eggs ranging from 7 to 334. Only one of the 21 ovigerous females collected in 1989 and 1990 had just a few hundred eggs. The overall incidence of ovigerous females, particularly those with new eggs, increased substantially in 1989 and 1990 and especially in 1991. At Goose I., no ovigerous females at all were included in samples until 1989, 4 years after they were transplanted. This indicates a high degree of acclimation or physiological adjustment to environmental conditions in St. Michael's Bay on the part of females, resulting in much less resorption of ripe ovaries and much more extrusion in recent years. However, loss of the entire clutch of eggs appeared to be still quite prevalent. Ovigerous females sometimes lose their entire clutch of eggs by molting (Ennis 1984b). This may have been a more common occurrence in later years, which could explain the near absence of tiny clutches compared with the high incidence observed in 1987 and 1988, and would also be consistent with a high incidence of new shells and advanced setal development among females in 1989 and 1990. Despite some physiological adjustment resulting in more extrusion, for most females the molting and reproductive cycles continued to be out of phase.

Embryonic development in lobsters proceeds slowly at temperatures below 6°C, and hatching can be delayed by as long as 6 months if temperature remains at 2–3°C throughout spring, summer, and autumn, although it will eventually occur, even at that temperature (Aiken and Waddy 1986). Perkins (1972) found that advanced embryos will develop more slowly than less advanced ones when held at the same temperature. In one specimen with 29-week-old eggs on 10 January held at the Boothbay Harbor Laboratory under local water conditions, there was no measurable development for an 18-week period starting in early December. Over most of the period, temperature ranged from 0.1°C to 1.5°C.

In St. Michael's Bay, bottom temperature drops below 6°C by mid-October, below 3°C by mid-November, and below 0°C by late November. Of the old-egged ovigerous specimens from there, which are presumed to have extruded the previous summer, there was one with 0.8 yolk remaining when examined at the end of June, three with 0.7 remaining around 20 July, and three with 0.5 remaining in mid-August. Possibly some of these females carry their eggs through a second winter and may represent the ones observed in our samples with sufficiently advanced development for hatching to occur before the end of summer (i.e., hatching 2 years after extrusion rather than the usual 1).

Only 6 of the 17 old-egged ovigerous females collected in St. Michael's Bay from 1986 to 1991 had less than half the yolk remaining in the eggs when examined. Four of these would likely have been ready for

hatching by sometime in September, around the time autumn cooling begins. The other, which had 0.3 yolk remaining and a PEI of 470 at the end of June, would probably have hatched by early August. This was the only specimen for which hatching as much as 4 or 5 weeks in advance of autumn cooling was a possibility. However, extensive plankton sampling (130 15-min tows with a 1 m diameter net) conducted near the sites where lobsters were released in St. Michael's Bay, from 28 July to 22 August 1986, and from 18 July to 30 August 1987, failed to produce lobster larvae.

Bottom temperature at 7 m in St. Michael's Bay during August ranged from around 9°C to 10.5°C. Assuming temperature in the surface layer was around 15°C, at which lobster larvae will reach Stage IV in 25 days (Templeman 1936), it is possible that larvae hatching in early August would be in Stage IV at the end of August and ready to settle by mid-September. Larvae hatching in late August would be exposed to temperatures below 10°C well in advance of reaching Stage IV. At 10°C, it takes 2 months from hatching to Stage IV; and at 5°C, larvae generally die without reaching Stage IV (Templeman 1936). Caddy's (1979) consideration of the influence of seasonal temperature regime on survival of lobster larvae indicates poor chances of survival if larvae have not reached Stage IV by the end of August. Any larvae hatching in St. Michael's Bay in late August–early September appear to have little chance of reaching Stage IV and settling in the area. The 1988–90 diver-collected samples involved 12 dives totaling about 30 diver hours searching at the Indian Arm and Goose I. sites. Not a single small lobster was found, suggesting there had been very little if any recruitment since lobsters were transplanted in 1982.

The possibility that the lobsters transplanted to St. Michael's Bay will become a self-sustaining population is remote. While the portion of females with ripe ovaries that actually extrude has increased substantially during this study, many of these lose all or most of their clutch of eggs before the following summer. Of those females that carry their eggs for at least a year, very few have eggs ready for hatching sufficiently early in the summer that any larvae are likely to settle in the area. Any local recruitment that might occur would be too little and too irregular to support a fishery for lobsters in St. Michael's Bay.

Citations

Aiken, D.E.
1973 Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 30:1337–1344.

Aiken, D.E., and S.L. Waddy
1976 Controlling growth and reproduction inthe American lobster. *In* Avaulk, J.W. Jr. (ed.), Proc., 7th Annu. meet. world maricult. soc., p. 415–430. Louisiana St. Univ. Press, Baton Rouge.
1980a Reproductive biology. *In* Cobb, J.S., and B.F. Phillips (eds.), The biology and management of lobsters, vol. 1, Physiology and behavior, p. 215–276. Academic Press, NY.
1980b Maturity and reproduction in the American lobster. *In* Anthony, V.C., and J.F. Caddy (eds.), Proc., Canada–U.S. workshop on status of assessment science for N.W. Atlantic lobster (*Homarus americanus*) stocks, p. 59–71. Can. Tech. Rep. Fish. Aquat. Sci. 932.
1982 Cement gland development, ovary maturation, and reproductive cycles in the American lobster, *Homarus americanus*. J. Crustacean Biol. 2:315–327.
1986 Environmental influence on recruitment of the American lobster, *Homarus americanus*: A perspective. Can. J. Fish. Aquat. Sci. 43:2258–2270.
1989 Interaction of temperature and photoperiod in the regulation of spawning by American lobsters, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 46:145–148.

Caddy, J.F.
1979 The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 204–216.

Conan, G.Y.
1986 Summary of session 5: Recruitment enhancement. Can. J. Fish. Aquat. Sci. 43:2384–2388.

Cooper, R.A., and J.R. Uzmann
1980 Ecology of juvenile and adult *Homarus*. *In* Cobb, J.S., and B.F. Phillips (eds.), The biology and management of lobsters, vol. II, p. 97–142. Academic Press, NY.

Ennis, G.P.
1981 Fecundity of the American lobster, *Homarus americanus*, in Newfoundland waters. Fish. Bull., U.S. 79:796–800.
1984a Incidence of molting and spawning in the same season in female lobsters, *Homarus americanus*. Fish. Bull., U.S. 82:529–530.
1984b Comparison of physiological and functional size-maturity relationships in two Newfoundland populations of lobsters *Homarus americanus*. Fish. Bull., U.S. 82:244–249.

Perkins, H.C.
1972 Development rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). Fish. Bull., U.S. 70:95–99.

Templeman, W.
1936 The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). J. Biol. Board Can. 2:485–497.
1940 The life history of the lobster. Newfoundland Dep. Nat. Resour., Serv. Bull. (Fish.) 15, 42 p.

Larval development, distribution, and ecology of cobia *Rachycentron canadum* (Family: Rachycentridae) in the northern Gulf of Mexico*

James G. Ditty
Richard F. Shaw

Coastal Fisheries Institute, Wetland Resources Building
Louisiana State University, Baton Rouge, Louisiana 70803-7503

Abstract. – Cobia is a highly prized recreational species of worldwide distribution in tropical and subtropical seas, but the development, distribution, and ecology of its early life stages are poorly known. Eggs are spherical, average 1.24 mm in diameter, and have a single oil globule (mean diameter 0.45 mm). The perivitelline space is narrow and the embryo heavily pigmented. Eggs hatch in about 24 h at 29°C based on the relationship between egg diameter and water temperature to predict development time in other marine fishes. Larvae hatch at about 2.5 mm SL. Cobia spawn in both estuarine and shelf waters during the day, and eggs and larvae are usually collected in the upper meter of the water column. Larvae are recognized by the large supraorbital ridge with a single spine, laterally swollen pterotics, heavy body pigmentation, minute epithelial spicules covering the body integument, and a pair of moderate-to-large, simple spines on either side of the angle of the posterior preoperculum. Only 70 larvae <20 mm SL were collected and identified from the Gulf of Mexico between 1967 and 1988; most occurred between June and September at surface temperatures ≥25°C, salinities >27‰, and within the 100 m depth contour. Similar patterns of head spination provide evidence of a sister-group relationship between cobia and dolphinfish rather than that previously hypothesized between cobia and remoras.

Manuscript accepted 16 July 1992.
Fishery Bulletin, U.S. 90:668–677 (1992).

Cobia, in the monotypic family Rachycentridae, is distributed worldwide in tropical and subtropical seas (Briggs 1960), except the eastern Pacific, and is found seasonally in temperate waters (Hassler and Rainville 1975). A highly prized recreational species, most of the U.S. landings are from Gulf of Mexico (Gulf) waters; they are also caught incidentally in commercial fisheries (Shaffer and Nakamura 1989). Recreational landings are not well documented, but cobia are reportedly not abundant and recruitment is considered low (Gulf of Mexico & S. Atl. Fish. Manage. Counc. 1985). Cobia are migratory and usually absent from commercial and recreational catches of the northern Gulf during late fall and winter at which time they are caught off the Florida Keys. They migrate north and west along the Gulf coast during the spring (Shaffer and Nakamura 1989) and reappear in northern Gulf waters during March and April (Springer and Pirson 1958). Cobia are usually caught in shallow coastal waters (Shaffer and Nakamura 1989), although they are often taken offshore along the Louisiana and Texas coasts in association with oil and gas platforms and rafts of *Sargassum* (RFS, pers. observ.).

Despite the recreational value of cobia, its ecology, distribution, and morphological development during early life stages are poorly known. Only 23 specimens <20 mm SL are reported in the historical literature for the Gulf (Dawson 1971, Finucane et al. 1978ab, Houde et al. 1979). Richards (1967) reviewed cobia general life history, Shaffer and Nakamura (1989) compiled biological data, and Hassler and Rainville (1975) developed techniques for hatching and rearing cobia. In addition, Johnson (1984) discussed the utility of cobia early life stages for examining previous phylogenetic hypotheses and the evolutionary interrelationships of echeneoids (Rachycentridae–Coryphaenidae–Echeneididae). Aspects of early egg development have been described (Ryder 1887, Joseph et al. 1964, Hassler and Rainville 1975) but not development of early larvae <12.6 mm SL. Most larval illustrations and photographs are of poor quality (Ryder 1887, Dawson 1971, Hassler and Rainville 1975, Finucane et al. 1978a, Johnson 1984). The objectives of this study are to describe cobia egg and larval development, to provide data on the seasonal occurrence, distribution, and ecology (i.e., relationship of larvae to water temperature, salinity, and station depth at time of capture) of early life stages of cobia in the Gulf, and to further examine the interrelationships of the echeneoids.

* Contribution LSU-CFI-91-6 of the Coastal Fisheries Institute, Louisiana State University.

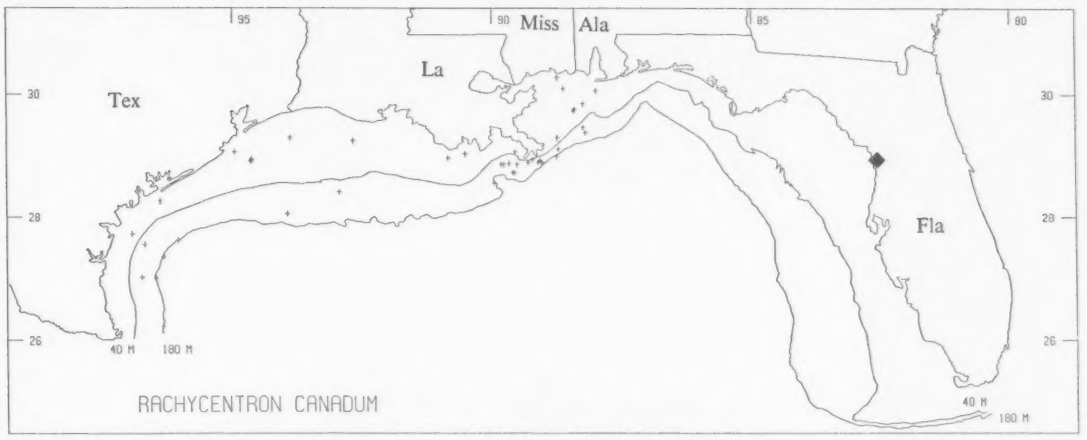


Figure 1

Distribution of larval cobia *Rachycentron canadum* in the northern Gulf of Mexico. Plus signs are positive catch stations; diamond is location of Crystal River estuary where cobia eggs and yolksac larvae were collected.

Methods

Eggs and larvae were obtained from museum collections along both the Gulf and Atlantic coasts. We examined 70 cobia eggs (all late-stage embryos) and 76 larvae 2.6–25 mm SL and determined their seasonal occurrence, distribution, and ecology. Hydrographic parameters were weighted by the total number of larvae caught at each station to derive mean and median values. All specimens were formalin-preserved except those from Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys of the Gulf which were in ethyl alcohol. We considered lat. 26°00′N as the southern boundary of our survey area (Fig. 1). Temperature and salinity data were from the surface only.

Body measurements were made to the nearest 0.1 mm with an ocular micrometer in a dissecting scope and follow Hubbs and Lagler (1958) and Richardson and Laroche (1979). All lengths refer to standard length (SL) unless otherwise noted. A compound scope was used to examine the origin and location of epithelial spicules. Representative specimens were illustrated with the aid of a camera lucida. Specimens were not cleared and stained because of the paucity of material. Fin rays were counted when their pterygiophores were visible; spines when they resembled formed structures (Richardson and Laroche 1979). Myomeres were difficult to count in fish >6 mm due to heavy larval pigmentation and opacity of the musculature, even under polarized light, but all specimens <6 mm had 24 myomeres. Cobia undergoing transition to the juvenile stage were those with a full complement of formed rays in all fins. Egg staging followed Moser and Ahlstrom (1985).

Egg and larval development

Cobia eggs were spherical and measured 1.15–1.3 mm ($\bar{x}$ 1.24, N 31), with a single oil globule 0.4–0.65 ($\bar{x}$ 0.45, N 13) in diameter. The oil globule was pigmented and lay near the vegetal pole opposite the developing embryo. The perivitelline space was narrow with the embryo occupying about 85% of egg volume (range 70–92%, N 13). The chorion was smooth and unornamented. Cobia eggs hatch in about 24 h at 29°C based on Pauly and Pullin's (1988) relationship between egg diameter and water temperature to predict development time in marine fishes.

The embryo of late-stage Gulf cobia eggs was heavily pigmented except for the caudal peduncle which was unpigmented. Late-stage embryos from north of Cape Hatteras, NC, had pigment lightly scattered over the peduncle. Early yolksac larvae (2.6–3.2 mm) were heavily pigmented externally and lacked a functional mouth, eye pigment, and all fins. A single oil globule with pigment was also present in the middle of the yolksac. External pigment occurred over the snout and in a band immediately behind the primordial eye. The eye remained unpigmented until larvae were 3.5–4.0 mm (Fig. 2). At higher magnification, tiny epithelial

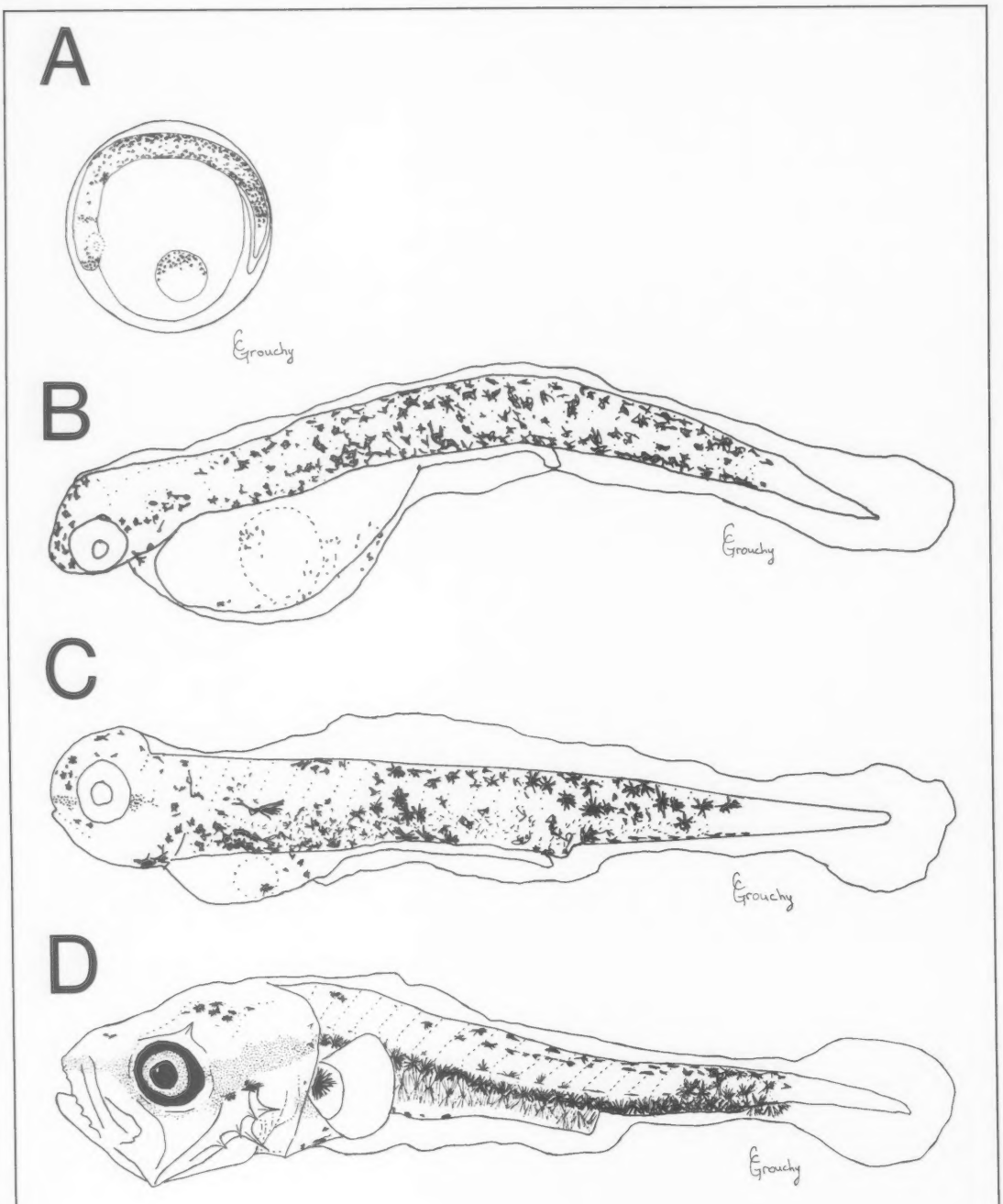


Figure 2

Eggs and larval development of cobia *Rachycentron canadum*. (A) Late-stage egg, diameter 1.24 mm; (B–C) yolksac larvae 2.6 and 3.0 mm SL; (D–H) larvae 4.5 mm, 6.8 mm, 10.0 mm, 14.1 mm, and 18.9 mm SL.

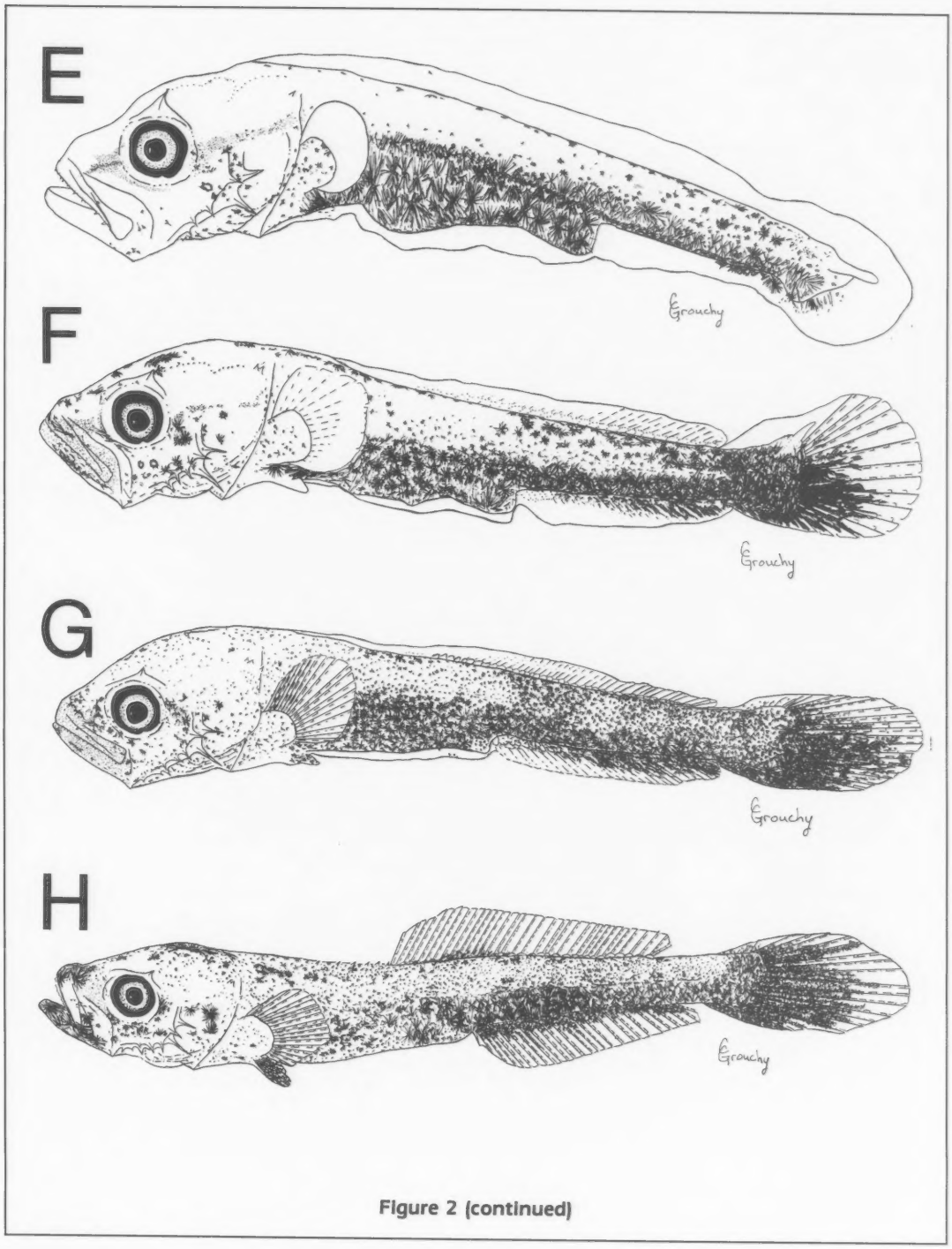


Figure 2 (continued)

Table 1
Body proportions of larval cobia *Rachycentron canadum* from the Gulf of Mexico, expressed as % standard length (SL).

SL	*N*	Preanal length	Head length	Snout length	Orbit diameter	Upper jaw length	Body depth cleithrum	Predorsal length	Prepelvic length	Peduncle length
2.6	1	61.5								
3.2	1	62.5								
4.0–4.9	2	64.4–65.0	27.8–31.2	6.7–7.5	10.0–11.2	10.0–13.8	18.9–21.2			
5.0–5.9	3	68.0–68.6	31.4–34.0	7.6–10.0	11.0–12.7	13.6	20.3–20.6		33.9	
6.0–6.9	3	63.2–67.2	27.9–31.7	7.3–8.3	8.8–10.8	10.3–12.7	19.8–23.3		30.9	
7.0–7.9	3	64.1–65.3	26.9–29.5	7.0–8.7	9.0–10.0	10.9–13.3	17.9–20.0	52.6	30.8–33.3	12.0–12.8
9.8	1	64.3	30.6	8.7	9.2	12.8	21.4	51.0	33.7	12.8
10.0–10.9	3	57.1–64.1	27.5–29.5	7.0–8.1	9.0–10.0	11.5–13.3	19.0–20.0	50.0–56.3	30.0–36.9	12.1–13.3
11.0–11.9	3	57.3–60.9	27.7–29.9	6.7–7.8	8.4–8.7	11.3–12.0	18.3–19.2	49.6–52.2	31.1–34.2	11.5–12.6
12.0–12.9	2	63.2–63.7	28.2–28.8	7.2–8.0	8.8–8.9	11.2–11.3	16.1–18.4	49.2–50.4	32.0–32.2	12.5–12.8
14.0–14.9	2	56.6–58.7	26.2–27.3	6.9–7.0	8.0–8.3	11.0–11.2	17.2–17.5	49.0–50.3	29.4–30.3	11.0–11.2
16.0–16.9	3	58.4–59.9	26.5–26.9	7.2–7.8	7.8–8.4	10.2–10.5	15.0–16.8	48.2–49.4	28.9–30.1	12.0–13.6
19.5	1	57.4	27.2	7.7	7.7	10.2	15.4	46.2	29.7	12.8
21.0	1	57.1	24.8	6.7	7.1	9.5	14.3	47.6	27.1	12.8
25.0	1	56.0	24.0	6.0	7.2	8.8	14.9	46.8	26.8	12.0

spicules were also visible over the entire body integument, except the pupil of the eye, by 4 mm.

Body measurements were made on 30 cobia larvae to examine developmental morphology (Table 1). Preanal length was 61.5–62.5% SL in yolksac larvae and increased slightly during preflexion, but decreased steadily thereafter. A single intestinal loop, visible through the body wall, gave the ventral visceral mass a bulbous appearance by 7 mm. Body depth was about 20% SL in larvae <10 mm but decreased to about 15% by 25 mm. Likewise, orbit diameter decreased from about 11–7% SL as larvae increased in length. Other body proportions were relatively stable until larvae were >10 mm. Thereafter, a slow but steady decline occurred in all proportions when compared with SL, except caudal peduncle length which remained constant (Table 1). The relationship between standard and total lengths (TL), as defined by regression analysis, was linear and highly correlated ($SL = 0.73TL + 1.44$; N 29, r^2 0.998) at all sizes.

The supraorbital ridge and two largest preopercular spines were visible by 4 mm, and the pterotics were laterally swollen. The two preopercular spines were located on either side of the angle of the posterior preopercle. Three smaller spines, the largest of which was inserted between the two posterior preopercular spines, were also present along the anterior preopercle. Spines were added along both the anterior and posterior preopercle until a total of 4 anterior and 4–5 posterior preopercular spines was reached by 14–15 mm. A single spine occurring along the supraorbital ridge of each frontal bone by 4.5 mm was directed posterolaterally by 6 mm. The supraorbital spine and swollen pterotics were best observed when viewed dorsally (see Hardy 1978 for illustration). A supracleithral spine also occurred about 10.5–11 mm, and two posttemporal spines (supratemporal of Dawson 1971) originating from a common base were visible by 12 mm. All head spination was simple and unserrated.

In early larvae, internal pigment on the roof of the mouth and ventral to the hindbrain and otic capsule formed a mediolateral stripe through the head. Externally, melanophores were scattered over the snout, fore- and midbrains, on the nape, and over the operculum. Pigment also occurred immediately anterior to the cleithral symphysis and along the isthmus. Both the tip of the quadrate bone and dentary remained unpigmented until 7–7.5 mm. Head pigmentation increased with length (Fig. 2). Minute epithelial spicules (Johnson 1984) covered the body by 4 mm, but were best observed on the head and larval finfold. Spicules were more easily observed on the integument as larvae increased in length.

Along the dorsal midline, a bilateral row of melanophores extended posteriorly from the nape to above the anus, behind which these rows coalesced to form a continuous band of postanal, dorsal pigment. By 4.5 mm, pigment occurred on the pectoral fin base, and larvae were sparsely pigmented dorsolaterally but heavily pigmented ventrolaterally. The caudal peduncle was unpigmented in early larvae, but pigment extended onto the peduncle by 5.5–6.5 mm and over the lower hypural bones by 7 mm. Pigment was also present on the posterior third of the anal finfold and proximally on the ventral caudal-fin rays by 7.5 mm. Body and anal- and caudal-fin ray pigment increased with length. Pigment occurred on the posterior dorsal-fin pteryio-

Table 2
Fin ray counts of larval cobia *Rachycentron canadum* from the Gulf of Mexico.

Size (mm SL)	*N*	Dorsal*	Anal	Pectoral	Pelvic
9.8	1	30	25	9	
10.0–10.9	3	27–30	22–25	12–13	
11.0–11.9	3	28–31	24–26	13–17	
12.0–12.9	2	30–33	24–26	14	
14.0–14.9	2	31	25	17	3
16.0–16.9	3	28–32	I,24–26	17–19	I,5
19.5	1	31	I,25	20	I,5
21.0	1	31	I,25	21	I,5
25.0	1	29	I,25	20	I,5

* Dorsal spines are virtually impossible to count on uncleared or unstained specimens.

phores by about 10.5 mm. Fin pigmentation progressed anteriorly along the dorsal base and extended onto posterior dorsal rays by about 18–19 mm. Pelvic rays were first pigmented at about 13 mm, but pectoral fins remained unpigmented at all sizes examined (Fig. 2).

A 49 mm juvenile had a jet black caudal fin except for the distal tips of the upper principal rays. Pelvic fins were completely black, but pigment was present basally on only the upper few rays of the pectoral fin. Pigment also covered all of the posterior rays of both the dorsal and anal fins. Fin pigment decreased anteriorly, however, such that only the basal portions of the anterior dorsal and anal rays were pigmented. All dorsal spines were visible and the integument was entirely jet black.

Fin development

A continuous median finfold extended posteriorly along the body from the nape to the cleithral symphysis of early larvae. About 5 mm, a ventral thickening occurred near the tip of the unflexed notochord. Anlagen began to form obliquely downward in the caudal finfold during flexion (~6.5–8 mm). As the hypural complex shifted to a terminal position, caudal ray development proceeded both dorsally and ventrally until the adult complement of 9+8 principal rays was present at 10.5–11 mm. By 19.5 mm, the caudal fin was distinctly spatulate and heavily pigmented. Dorsal- and anal-fin-base development coincided with notochord flexion. These fin bases began to differentiate centrally, and development proceeded both anteriorly and posteriorly with all pteryiophores countable by 10–11 mm in both fins. Dorsal- and anal-ray anlagen, however, began to develop along the posterior fin base and proceeded anteriorly. Development of anal rays consistently preceeded that of dorsal rays. All anal fin elements were countable by 17 mm. Dorsal spines were very difficult to count in specimens not cleared and stained because spines were short and often covered by integument. One partially cleared 16.7 mm specimen had 7 poorly-formed, short dorsal spines, 11 precaudal and 14 caudal vertebrae (including urostyle), and 7 branchiostegal rays. Pelvic buds were visible by 6 mm, with the full complement of elements (I,5) present by 16.5–17 mm. Pectoral rays were first visible at about 10 mm and the full complement (20–21 rays) was present by 19–20 mm. A full complement of rays in all fins (around 20 mm) marked the beginning of transition to the juvenile stage (Table 2).

Distribution and ecology

The only confirmed collection of both cobia eggs and yolksac larvae from the Gulf was from the Crystal River estuary, Florida, during July 1984. These specimens were collected from waters 28.1–29.7°C and 30.5–34.1‰, except for a single 3.2 mm yolksac larva from a power plant discharge canal at 36.7°C and 25.2‰. All other eggs and early larvae were from stations along the outer perimeter of the study area at station depths of 3–6 m. No eggs or larvae were collected at stations located over oyster reefs, in the salt marsh, or in tidal creeks. Gulfwide, larvae were first collected during late May, with most (98%) collected June–September. Cobia larvae also primarily (85%) occurred at 25–30°C ($\bar{x}$ 28.2°C, range 24.2–32.0°C), at >27‰ ($\bar{x}$ 30.8‰, range 18.9–37.7‰), and most (75%) at station depths <100 m (median 50 m, range 3.1–300 m) (Fig. 3).

Discussion

Our data suggest that cobia eggs hatch in about 24 h at 29°C. Ryder (1887) projected a 36 h incubation time at an unspecified temperature. Based on Pauly and Pullin's (1988) predictive relationship to derive incubation time and a mean egg diameter of 1.24 mm from this study, Ryder's cobia eggs were probably incubated at about 25°C. In cooler waters of the mid-Atlantic Bight and northward during the spring/early summer (i.e., ~20°C), projected incubation time increases to 56 h. Cobia hatch at about 2.5 mm based on collection of wild-caught early yolksac larvae (2.6–3.2 mm) with unpigmented eyes and on the work of Hassler and Rainville (1975).

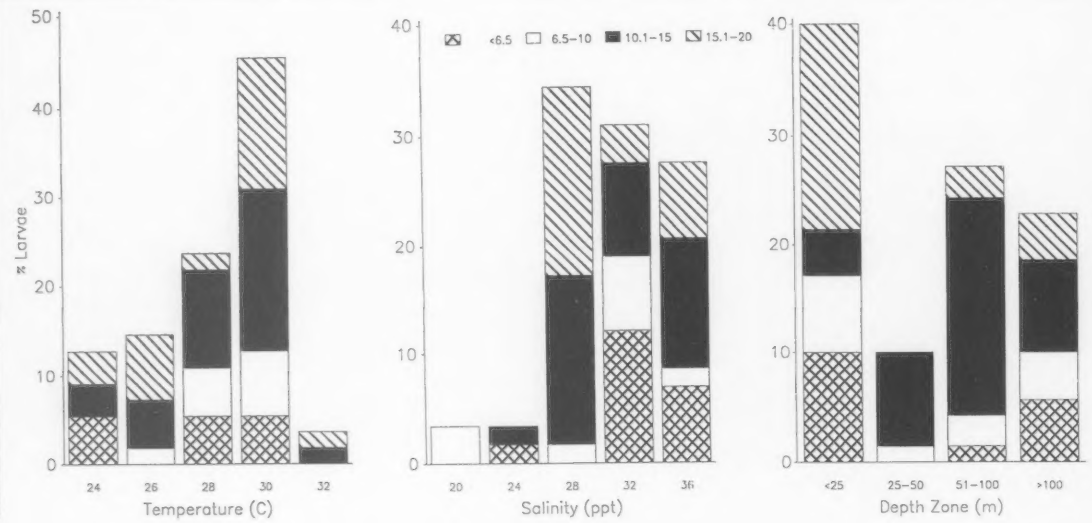


Figure 3

Distribution of cobia *Rachycentron canadum* larvae in the Gulf of Mexico with respect to hydrography. Larval stage/length class was assigned as follows: preflexion, <6.5 mm SL; flexion/early postflexion, 6.5–10.0 mm SL; late postflexion, 10.1–15.0 mm SL; and transition larvae, 15.1–20.0 mm SL.

Our data on egg and oil globule diameter agree with historical data (Ryder 1887, Joseph et al. 1964, Richards 1967, Hassler and Rainville 1975) except that our mean oil globule diameter (0.45 mm) is greater than that found for eggs from the Chesapeake Bay area (0.37 mm, Richards 1967; 0.38 mm, Joseph et al. 1964). Only two cobia eggs are previously illustrated, one in early- and the other in midstage development (Ryder 1887). The diameter of the early-stage egg, however, is considerably smaller than that of the midstage egg, and the specific identification of the early egg is unclear.

Cobia spawn during the day, since all embryos examined from the Gulf are at similar stages of development (i.e., late stage after Ahlstrom and Moser 1980) when collected during midmorning, except for one collection of late-stage eggs near midnight. Furthermore, daytime spawning cobia have been reported about 48 km southwest of Panama City, Florida (see Shaffer and Nakamura 1989 for details) in waters we estimate at 82–165 m deep. Our data also show that cobia larvae occur in both estuarine and shelf waters of the Gulf (Figs. 1,3), primarily during May–September. The only confirmed cobia eggs and yolksac larvae collected together in the Gulf are from the Crystal River estuary at station depths of 3–6 m. Early larvae (≤6.8 mm) are also collected at stations within the 65–134 m isobath range off Texas during September (Finucane et al. 1978b). The location of these collections suggests that some spawning also occurs on the shelf 50–90 km from the coast. Offshore waters beyond the edge of the continental shelf are relatively well sampled during May (SEAMAP 1983–87) when histological analyses indicated adult cobia are ripe (Thompson et al. 1991), but no cobia larvae were identified. Seven cobia larvae (all >9.5 mm) were identified from beyond the 180 m depth contour during this study and all were collected off the Mississippi River delta. Distribution of larvae centered around the Mississippi River delta, however, may reflect the intensity of neuston net sampling in this area rather than actual distribution of spawning adults. Only two larvae were collected off Florida during a comprehensive multiyear survey of eastern Gulf waters >10 m, both during August (Houde et al. 1979).

Seasonal occurrence and ecological data from along the Atlantic coast of the United States support our findings from the Gulf. Cobia eggs occur primarily between May and August at surface water temperatures >20°C (Joseph et al. 1964, Hassler and Rainville 1975, Eldridge et al. 1977; W.F. Hettler and L. Settle, NMFS Southeast Fish. Sci. Cent., Beaufort NC, pers. commun.; P. Berrien, NMFS Northeast Fish. Sci. Cent., Sandy Hook NJ, pers. commun.; D. Hammond, S.C. Dep. Wildl. Mar. Resour., Charleston SC, pers. commun.). Eggs are collected in lower Chesapeake Bay (Joseph et al. 1964), inlets to North Carolina estuaries

(W.F. Hettler and L. Settle, pers. commun.), in coastal waters 20–49 m deep (App. Table 1), and both near the edge of the Florida Current and in the Gulf Stream (Hassler and Rainville 1975, Eldridge et al. 1977). Off North Carolina, cobia eggs are usually collected on flood tides but few larvae are found in tidal inlets (W.F. Hettler and L. Settle, pers. commun.). Cobia eggs and larvae are usually collected in the upper meter of water with surface-towed nets (Joseph et al. 1964, Hassler and Rainville 1975 [implied], Eldridge et al. 1977; W.F. Hettler, pers. commun.). Neither cobia study off the Atlantic coast of the United States (Joseph et al. 1964, Hassler and Rainville 1975) provides environmental data, but eggs are successfully hatched at 19–35‰ (Hassler and Rainville 1975).

Similarities in larval morphology provide evidence of a sister-group relationship between cobia and dolphinfishes (Coryphaenidae) rather than that previously hypothesized between cobia and remoras (Echeneididae) (Johnson 1984). Larvae of both cobia and the dolphinfishes share similar patterns of head spination: laterally swollen pterotics; a single, simple spine on the supraorbital ridge of each frontal bone (except in pompano dolphin *C. equiselis*, which may have multiple spines along the ridge; JGD, pers. observ.); a small posttemporal spine; and several spines along the anterior and posterior preopercule, including an enlarged spine on either side of the angle. However, cobia have a small supracleithral spine (Dawson 1971, this study) that dolphinfishes lack. Remoras completely lack head spines. Both cobia and the dolphinfishes have epithelial spicules, a specialization unique to larvae of these species (Johnson 1984). We found spicules visible on the integument of both cobia and the dolphinfishes by 4 mm (JGD, pers. observ.) and they cover the entire body surface, except the pupil of the eye. Spicule composition and function, however, are unknown (Johnson 1984). Larval cobia are further separated from superficially similar remoras by the presence of large hook-like teeth on the dentary in remoras. Cobia lack these teeth. Larval cobia differ from the dolphinfishes by the lack of dorsal and anal spines and a higher vertebral count in the dolphinfishes (25 in cobia vs. 30–34 in dolphinfishes). Dolphinfishes also usually have 50+ soft dorsal rays, whereas cobia have 27–33.

Acknowledgments

This study was supported by the Marine Fisheries Initiative (MARFIN) Program (contract nos. NA90AA-H-MF111 and NA90AA-H-MF727). Thanks to those who loaned us specimens or provided data: Karen Burns, Mote Marine Lab, Sarasota FL; John Caruso, Tulane University Museum, New Orleans LA; L. Alan Collins and Churchill Grimes, NMFS Southeast Fisheries Science Center, Panama City FL; Wayne Forman and Leroy Kennair, Freeport-McMoRan, New Orleans LA; Bruce Comyns and Stuart Poss, Gulf Coast Research Lab, Ocean Springs MS; Peter Berrien, NMFS Northeast Fisheries Science Center, Sandy Hook NJ; Bill Hettler and Larry Settle, NMFS Southeast Fisheries Science Center, Beaufort NC; and Karsten Hartel, Museum of Comparative Zoology at Harvard. Thanks also to the Southeast Area Monitoring and Assessment Program (SEAMAP) and the Gulf States Marine Fisheries Commission for providing specimens and environmental data; to the Marine Resources, Monitoring, Assessment and Prediction (MARMAP) program for providing eggs collected during ichthyoplankton surveys; to Cathy Grouchy for illustrating the egg and larvae; and to Joe Cope for computer assistance.

Citations

Ahlstrom, E.H., and H.G. Moser
1980 Characters useful in identification of pelagic marine fish eggs. Calif. Coop. Oceanic Fish. Invest. Rep. 21:121–131.

Briggs, J.C.
1960 Fishes of worldwide (circumtropical) distribution. Copeia 1960(3):171–180.

Dawson, C.E.
1971 Occurrence and description of prejuvenile and early juvenile Gulf of Mexico cobia, *Rachycentron canadum*. Copeia 1971(1):65–71.

Eldridge, P.J., F.H. Berry, and M.C. Miller III
1977 Test results of the Boothbay neuston net related to net length, diurnal period, and other variables. S.C. Mar. Resour. Cent. Tech. Rep. 18, 22 p.

Finucane, J.H., L.A. Collins, and L.E. Barger
1978a Determine the effects of discharges on seasonal abundance, distribution, and composition of ichthyoplankton in the oil field. *In* Jackson, W.B. (ed.), Environmental assessment of an active oil field in the northwestern Gulf of Mexico, 1977–1978. NOAA Rep. to EPA (EPA-IGA-D5-E693-EO), NMFS Southeast Fish. Sci. Cent., Galveston, 299 p.

Finucane, J.H., L.A. Collins, L.E. Barger, and J.D. McEachran
1978b Ichthyoplankton/mackerel eggs and larvae. Environmental studies of the south Texas outer continental shelf, 1977. Final Rep. to Bur. Land Manage. by NMFS Southeast Fish. Sci. Cent., Galveston, 504 p.

Gulf of Mexico & South Atlantic Fishery Management Councils
1985 Final Amendment 1, fishery management plan and environmental impact statement for coastal pelagic resources (mackerels) in the Gulf of Mexico and south Atlantic region. Gulf Mex. Fish. Manage. Counc., Tampa, FL.

Hardy, J.D. Jr.
1978 Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval, and juvenile stages. Vol. III. Aphredoderidae through Rachycentridae. U.S. Fish. Wildl. Serv., Biol. Serv. Prog. FWS/OBS-78/12, 394 p.

Hassler, W.W., and R.P. Rainville
1975 Techniques for hatching and rearing cobia, *Rachycentron canadum*, through larval and juvenile stages. Univ. N.C. Sea Grant Coll. Prog., UNC-SG-75-30, Raleigh, 26 p.

Houde, E.D., J.C. Leak, C.E. Dowd, S.A. Berkeley, and W.J. Richards
1979 Ichthyoplankton abundance and diversity in the eastern Gulf of Mexico. Univ. Miami Rep., BLM Contract AA550-CT7-28, Miami, 546 p.

Hubbs, C.L., and K.F. Lagler
1958 The fishes of the Great Lakes region. Univ. Mich. Press, Ann Arbor, 213 p.

Johnson, G.D.
1984 Percoidei: Development and relationships. *In* Moser, H.G., et al. (eds.), Ontogeny and systematics of fishes, p. 464–498. Spec. Publ. 1, Am. Soc. Ichthyol. Herpetol., Allen Press, Lawrence, KS.

Joseph, E.B., J.J. Norcross, and W.H. Massmann
1964 Spawning of the cobia, *Rachycentron canadum*, in the Chesapeake Bay area, with observations of juvenile specimens. Chesapeake Sci. 5:67–71.

Moser, H.G., and E.H. Ahlstrom
1985 Staging anchovy eggs. *In* Lasker, R. (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 37–41. NOAA Tech. Rep. NMFS 36.

Pauly, D., and R.S.V. Pullin
1988 Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environ. Biol. Fish. 22(4):261–271.

Richards, C.E.
1967 Age, growth, and fecundity of the cobia, *Rachycentron canadum*, from Chesapeake Bay and adjacent mid-Atlantic waters. Trans. Am. Fish. Soc. 96(3):343–350.

Richardson, S.L., and W.A. Laroche
1979 Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (Family Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:1–46.

Ryder, J.A.
1887 On the development of osseous fishes, including marine and freshwater forms. Rep. U.S. Fish. Comm., Pt. 13, 1885 (1887):489–604.

SEAMAP (Southeast Area Monitoring and Assessment Program)
1983–87 Plankton data for 1982–1986. Fisheries-independent survey data/National Marine Fisheries Service, Southeast Fisheries Center. Produced by Gulf States Mar. Fish. Comm., Ocean Springs, MS (ASCII file).

Shaffer, R.V., and E.L. Nakamura
1989 Synopsis of biological data on the cobia *Rachycentron canadum* (Pisces: Rachycentridae). NOAA Tech. Rep. NMFS 82 [FAO Fish. Synop. 153], 21 p.

Springer, V.G., and J. Pirson
1958 Fluctuations in the relative abundance of sport fishes as indicated by the catch at Port Aransas, Texas 1952–1956. Publ. Inst. Mar. Sci., Univ. Tex. 5:169–185.

Thompson, B.A., C.A. Wilson, J.H. Render, and M. Beasley
1991 Age, growth, and reproductive biology of greater amberjack and cobia from Louisiana waters. Year 1. Rep. to U.S. Dep. Commer., NOAA, NMFS, Coop. Agreement NA90AA-H-MF089, under Mar. Fish. Initiative (MARFIN) Prog., Coastal Fish. Inst., Louisiana St. Univ., Baton Rouge, 55 p.

Appendix Table 1

Station location, collection, and environmental data for cobia *Rachycentron canadum* eggs and larvae. All specimens from the Gulf of Mexico, except those loaned by the MCZ at Harvard and eggs from the NMFS Southeast Fisheries Science Center, Beaufort NC. Water temperature and salinity values were at the surface. NA = data not available.

Station	Date	Lat.	Long.	Stn. depth (m)	Temp. (°C)	Salinity ‰	Gear	*N*	Size (mm SL)	Eggs
4353[1]	6-05-67	30°13	88°47	11	25.9	28.9	7	2	16.6–18.2	
4357	6-05-67	30°02	88°40	18	26.4	29.4	7	1	17.0	
4355	6-10-68	29°24	88°17	55	32.0	36.6	7	2	12.6–15.3	
4356	6-12-67	29°19	88°14	73	30.3	27.8	7	3	13.6–14.2	
4354	6-18-68	29°42	88°27	37	29.4	37.7	7	1	12.9	
00807[1]	6-23-71	29°40	88°28	20	NA	NA	8	1	17.0	
01613	May/Jun 67	27°40	96°59	20	NA	NA	8	1	7.8	
01614	May/Jun 76	28°12	96°27	22	NA	NA	8	1	16.7	
01687	May/Jun 76	27°30	96°45	45	NA	NA	8	3	9.8–12.5	
EPA IV-A[2]	7-13-77	28°51	94°42	17	24.8	33.0	9	2	6.0–12.4	
EPA V-A	7-13-77	28°52	94°41	17	24.8	33.5	9	1	16.6	
EPA V-B	7-13-77	28°51	94°42	17	24.7	33.0	9	1	16.6	
EPA V-D	7-13-77	28°51	94°42	17	24.5	32.8	9	1	13.0	
EPA II-B	7-14-77	28°53	94°41	17	25.5	34.0	9	1	19.5	
BLM II-3[2]	7-06-77	27°18	96°23	131	>25	36.0	10	1	3.8	
BLM III	9-07-75	26°57	96°32	106	<25	36.0	11	1	5.9	
BLM IV-3	9-07-77	26°10	96°24	91	>25	36.0	10	1	12.4	
BLM III-2	9-08-77	26°58	96°48	65	>25	36.0	10	1	6.8	
BLM I-3	9-10-77	27°37	96°06	134	24.2	36.2	10	2	5.0–5.1	

Appendix Table 1 (continued)

Station	Date	Lat.	Long.	Stn. depth (m)	Temp. (°C)	Salinity ‰	Gear	*N*	Size (mm SL)	Eggs
9114 A-2[3]	7-18-84	28°56	82°35	4.6	29.6	31.5	12	1	6.8	14
9121 C-1	7-18-84	28°56	82°35	4.0	36.7	25.2	12	1	3.2	
9179 H-3	7-18-84	28°56	82°35	5.8	29.7	32.6	12	1	7.5	16
9008 H-4	7-18-84	28°56	82°35	6.1	29.7	32.6	12	1	3.1	
9266 I-1	7-18-84	28°56	82°35	6.0	29.4	31.3	12	1	2.6	6
9545 I-2	7-31-84	28°56	82°35	3.7	28.1	30.5	12	2	2.6–4.0	20
9086 I-2	7-18-84	28°56	82°35	4.1	29.6	34.1	12	–	–	4
9584 K-2	7-31-84	28°56	82°35	3.1	28.2	32.2	12	1	4.5	
3088[4]	6-14-84	28°58	90°33	13	28.0	18.9	13	2	6.7–7.8	
5370	6-18-86	28°54	90°53	7	29.7	27.9	10	1	10.5	
426	6-18-82	29°11	92°43	19	29.5	27.6	13	3	16.0–19.5	
432	6-23-82	29°14	93°56	15	NA	30.2	13	1	22.3	
573	6-16-82	28°30	90°00	100	29.4	33.3	10	1	5.0	
1644	6-07-83	30°00	88°02	26	25.0	NA	13	1	12.5	
1647	6-08-83	29°47	88°17	33	25.0	24.0	13	1	12.0	
3166	6-24-84	29°00	95°00	15	30.5	27.2	13	3	16.0–21.0	
3220	7-13-84	28°21	93°00	53	30.3	29.3	13	1	25.0	
4484	9-17-85	29°00	89°36	27	27.3	27.3	13	1	10.3	
94374[5]	6-01-85	34°54	75°40	33	NA	NA	NA	1	6.0	
94505	8-21-68	38°07	70°03	NA	NA	NA	NA	4	10.0–14.5	
AL8507-142[6]	7-28-85	36°50	75°27	21	25.0	31.9	14	–	–	2
AL8507-143	7-28-85	37°06	75°11	36	25.0	32.7	14	–	–	1
DL8604-83	6-21-86	38°38	74°48	20	20.2	31.9	14	–	–	1
DL8604-152	6-25-86	36°47	75°14	26	22.4	32.4	14	–	–	1
EK8006-1	7-16-80	35°41	74°58	49	25.2	36.0	14	–	–	1
EK8006-2	7-16-80	35°16	75°14	24	26.6	35.7	14	–	–	8
P-1[2]	9-12-86	28°48	89°52	82	29.8	27.0	13	1	10.1	
P-5	9-13-86	28°40	89°39	96	28.4	33.0	13	1	11.8	
P-17	9-25-86	28°53	89°16	63	28.6	33.0	13	1	11.0	
P-23	9-25-86	28°50	89°05	195	29.4	34.0	13	4	10.2–18.5	
P-31	9-26-86	28°56	88°48	300	28.6	34.0	13	2	10.7–12.3	
4[2]	5-27-88	29°14	88°47	63	25.1	31.7	13	1	9.5	
31	5-29-88	28°48	89°34	78	25.2	30.3	13	1	12.2	
12	8-26-88	28°40	89°37	101	29.0	NA	13	2	10.0–14.0	
24	8-26-88	28°49	89°43	70	28.8	26.8	13	2	14.0–19.0	
39	8-27-88	28°50	89°21	72	30.1	29.5	13	1	13.0	
44	8-27-88	28°52	89°07	111	29.6	28.0	13	3	10.0–24.5	
45	8-28-88	28°50	89°09	203	29.6	30.5	13	1	9.5	
60	8-27-88	29°03	88°46	157	29.5	29.5	13	1	15.0	

Stations:
[1]Gulf Coast Research Lab, Ocean Springs MS
[2]NMFS, Panama City Lab
[3]Mote Marine Lab, Sarasota FL
[4]SEAMAP 1982–1986
[5]Museum of Comparative Zoology, Harvard
[6]NMFS, Sandy Hook Lab, NJ

Gear:
[7]1 m, surface tow
[8]Neuston net (size unknown)
[9]0.5×1.0 m neuston net, 0.505 mm mesh
[10]60 cm bongo, 0.333 mm mesh, oblique tow
[11]1 m, 0.250 mm mesh, oblique tow
[12]1 m, stepped-oblique tow, 0.505 mm mesh
[13]1×2 m neuston net, 0.948 mm mesh
[14]60 cm bongo, 0.505 mm mesh, oblique tow

Energetics of associated tunas and dolphins in the eastern tropical Pacific Ocean: A basis for the bond

Elizabeth F. Edwards

Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, California 92038

Abstract. – The basis for the curious association between yellowfin tuna *Thunnus albacares* and spotted dolphin *Stenella attenuata* in the eastern tropical Pacific Ocean has never been explained. Consideration of the bioenergetics of the associated tuna and dolphins suggests that the association may be based on the combined effects of a shallow thermocline, overlapping size (length) ranges of associated yellowfin and young dolphins, congruent diets, hydrodynamic constraints on swimming speeds of dolphin schools, and social (caregiving) behavior of dolphins. Insights developed during construction and exercise of comparative bioenergetics models for the tuna and dolphin suggest that tunas are more likely to follow dolphins than dolphins to follow tunas, and that the strength of the association in a given area may be related to oceanographic conditions affecting prey distribution and abundance.

Manuscript accepted 29 July 1992.
Fishery Bulletin, U.S. 90:678–690 (1992).

In the eastern tropical Pacific Ocean, yellowfin tuna *Thunnus albacares* and spotted dolphin *Stenella attenuata* form an association strong enough that the fish can be captured by capturing the associated dolphins (e.g., Orbach 1977). The dolphins, easier to locate than the tuna, form the sighting cue for locating tuna schools. Despite chases lasting on average about half an hour (and occasionally as long as 2–3 hours) the fish tend to remain with the dolphins throughout. Eventually the dolphins tire and can be encircled, along with the associated tunas, with a purse-seine net.

Although the subject of substantial conjecture (e.g., Perrin 1969, Orbach 1977, Au and Pitman 1986, Au 1991), no definitive explanation exists for the association, perhaps in part because conjectures to date have been qualitative rather than explicitly quantitative. Quantifying the advantages or disadvantages of the association in terms of the energetics of its component groups holds promise for helping understand the bond, because such quantification can more readily expose conceptual errors, lead to unexpected insights, and form the basis for testable hypotheses. Expressing relationships in terms of energy flow (e.g., cost of finding food, cost of reproduction, feeding requirements, etc.) has often proved a useful format for developing understanding of biological phenomena. Following this precedent, I present here bioenergetics models for both tunas and dolphins in a "typical" association in the eastern tropical Pacific Ocean. I use these models to estimate feeding rates of tuna and dolphins, and discuss implications concerning the ecological advantage to tuna (or dolphins) when associated with dolphins (or tuna).

Estimates of forage requirements predict that tuna and dolphins should experience severe competition under some circumstances of prey distribution and abundance, but perhaps not under others. Observations of overlaps in sizes between associated tuna and dolphins and of morphological similarities between the animals have implications for the importance of swimming energetics to the association.

These estimated forage requirements and considerations about swimming energetics are discussed in terms of their implications for determining which component (tuna or dolphins) controls the association, how the competition might be mitigated, when the association might be more likely to occur, and how these factors might be used to locate large yellowfin tuna unassociated with dolphins. The last point is important in relation to current interest in eliminating the practice of "dolphin-fishing" in the eastern tropical Pacific Ocean. "Dolphin-fishing" involves location and capture of tuna schools by locating and capturing associated dolphin schools; as air-breathers, the dolphins are more easily sighted than the tuna due to the dolphin's surface activity. Other explanations for the bond, and poten-

tial conflicting evidence, are discussed briefly as they relate to the energetics models and results presented here.

Methods: Model development and description

The tuna-dolphin association

The tuna-dolphin association occurs in the eastern tropical Pacific Ocean (ETP) in a triangular region roughly the size of the continental United States (~10 million km^2), extending along the western coast of the Americas from the tip of Baja California (~20°N) south to Peru (~20°S) and seaward to ~140°W (Fig. 1). Total productivity in this area tends to be low relative to all other oceans, but high relative to other tropical oceans. Ocean currents and winds generate a typical pelagic environment in which areas of high productivity are distributed in dynamic, nonrandom, complex patterns (Fiedler et al. 1990, Fiedler 1992).

The ETP is characterized by an exceptionally shallow surface mixed layer. In contrast to other areas of the equatorial Pacific where the thermocline is generally 150–200 m deep (Kessler 1990), the depth of the thermocline layer throughout much of the ETP extends only 50–100 m below the surface (Fig. 1). Water temperatures in this wind-mixed layer are quite warm (25–30°C) and oxygen concentrations are high (Wyrtki 1966 and 1967, Fiedler et al. 1990, Fiedler 1992). Below this layer, water temperatures fall relatively rapidly (from ~27 to ~15°C) through the thermocline (usually 5–25 m vertical extent), stabilizing again below the thermocline (Fiedler et al. 1990). Oxygen concentrations also decrease relatively rapidly through the thermocline, increasing again in cold water at greater depths.

Strong dependence on warm water and on high concentrations of oxygen apparently force both tuna and dolphins into this unusually shallow mixed layer. Tuna must swim more or less constantly both to provide an adequate flow of sufficiently-oxygenated water over their gills and to locate adequate food supplies (e.g., Magnuson 1978, Olson and Boggs 1986). Yellowfin tuna would likely have difficulty maintaining an adequate energy balance swimming in the colder waters below the mixed layer, nor can they afford being caught for long in the oxygen minima characteristic of the thermocline.

Dolphins are constrained to reside near the ocean surface in order to breathe. Only temporary excursions below the mixed layer are tolerable, both because of this requirement for gaseous oxygen and because the blubber layer of the tropical dolphins involved in the tuna-dolphin association is too thin to maintain thermoneutrality in waters much colder than that in the mixed layer (unpubl. estimates). This is not necessarily a disadvantage, as the major prey for associated tuna and dolphins (small fish and squid; Perrin et al. 1973) also tend to concentrate in this upper mixed layer, at least periodically throughout a 24-hour day.

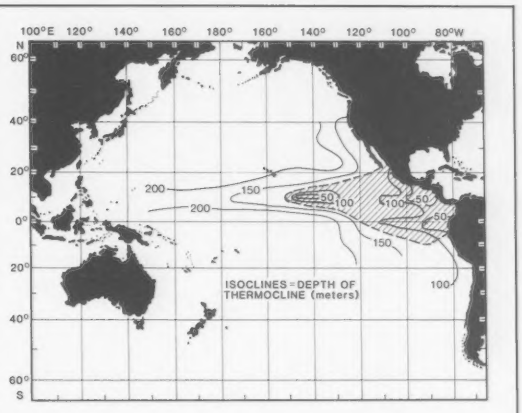


Figure 1

Depth of mixed layer in the area of the eastern tropical Pacific Ocean characterized by associations between yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata*. Tuna-dolphin fishery occurs roughly in area delimited by the 300 m isocline.

Although any individual tuna-dolphin association is doubtless dynamic in the details of its spatial configurations and component individuals, the association in general can be envisioned as a loose aggregation of animals characterized by dolphins swimming relatively near the ocean surface, separated vertically from the tuna swimming below by only a few meters (Fig. 2).

Although several species of dolphins and two species of tuna have been found to associate in the ETP, one species of dolphin (spotted dolphin *Stenella attenuata*) and one species of tuna (yellowfin *Thunnus albacares*) comprise the majority (>80%) of the associations (e.g., Orbach 1977, IATTC 1989). The remainder of this paper assumes the "tuna-dolphin association" includes only these two groups.

Energetics models

Both models followed the same format, using the standard bioenergetics approach of balancing food requirements against estimated energy costs for metabolism and energy savings as growth in biomass (University of Wisconsin Sea Grant 1989). The Wisconsin bioenergetics model derives estimates of consumption by

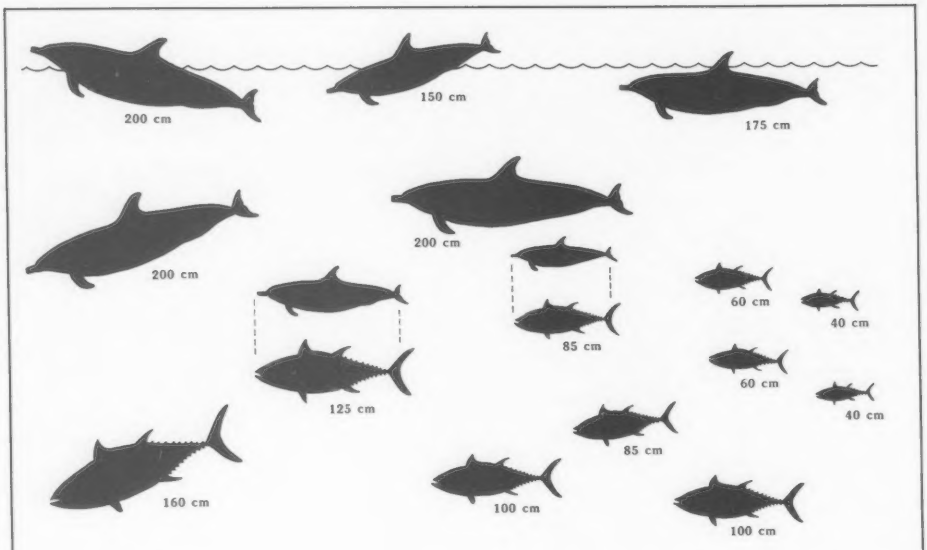


Figure 2
Idealized representation of a typical association of yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata*. Sizes and size-frequencies of tuna and dolphins are representative. Overlap in sizes between age-III yellowfin and neonate–1st yr dolphins (85–125 cm TL) is emphasized.

iteratively fitting an energetics equation for growth in body weight over time, to observed growth-rate curves derived from field samples of the organism in question. When the model growth curve simulates well the observed growth curve, the other fluxes estimated by the model are presumed to be reasonably accurate.

Specific rates (calories of flux · calories of animal^{-1} · day^{-1}) of energy flux were estimated based on data derived from various sources for individual tunas and dolphins as a function of size. Rates of energy flux for schools of dolphins and tuna were estimated as the sum of weight-specific estimates for individuals in each group.

Costs of reproduction were ignored for both yellowfin and spotted dolphins; in the yellowfin model because the model focuses on the sizes of yellowfin associated with dolphins, which tend to be relatively immature fish. Spawning activity in yellowfin does not occur in fish much smaller than 80 cm, and increases slowly to the maximum activity in fish larger than ~150 cm (Joseph 1963). Energy costs of reproduction for spotted dolphins were omitted because the fraction of pregnant, lactating, or pregnant and lactating females in a typical school at any time is relatively small (~25%; see School composition).

Some of the energetics parameters reported here for spotted dolphins are based on morphological measurements from 4 dolphin specimens from the ETP; 3 spotted dolphins measuring 81–189 cm total length (TL), plus 1 spinner dolphin *Stenella longirostris* 114 cm in length. The 81 cm individual was a very late-term fetus carried by the 189 cm animal. Although this sample is very small, all morphological measurements from these 4 animals fall well within the bounds of size-related regressions of morphological characteristics derived subsequently for a sample of 34 spotted dolphins measuring 74–215 cm TL (tip of rostrum to fluke notch) (unpubl. data).

School composition The yellowfin model addresses only those sizes of yellowfin found associated with dolphins (relatively large age-II and age-III fish, 55–125 cm TL; Fig. 3). Based on catch records from the fishery, an "average" association was assumed to include 500 yellowfin with an age composition of 65% age-II and 35% age-III fish per school (Ashley Mullin, IATTC, c/o Scripps Inst. Oceanogr., La Jolla; unpubl. data from commercial fishery).

Dolphin school composition was assumed to reflect the apparent age distribution of the spotted dolphin population, which in turn was assumed to appear as the length (age) distribution of dolphins collected during purse-seining operations in the ETP (Smith 1979, Barlow and Hohn 1984; A. Hohn, NMFS Southwest

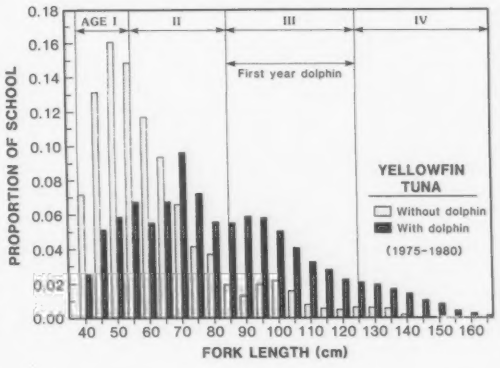


Figure 3

Sizes and ages of yellowfin tuna *Thunnus albacares* caught with and without dolphins in the eastern tropical Pacific Ocean, and length-interval during the first year of life by spotted dolphins *Stenella attenuata*. Data include all years 1975–84, all areas fished, all fleets (U.S. plus non-U.S.). (Unpubl. data from Ashley Mullin, IATTC, La Jolla).

Fish. Sci. Cent., La Jolla, unpubl. data). Proportions of nursing calves (ages 0–2 yr), adolescents (ages 3–14 yr), sexually adult males (ages 15 and up), and sexually adult females (ages 11 and up) in an average school were 0.05, 0.40, 0.25, and 0.30, respectively. Proportions of adult females not pregnant or lactating, lactating, pregnant, and pregnant and lactating animals were 0.05, 0.15, 0.08, and 0.02, respectively.

Weight-length conversions The tuna model used, as the calibration growth curve, the Gompertz fit derived by Wild (1986) for yellowfin tuna from the ETP. When necessary, body fork lengths in centimeters (cm FL) were converted to wet weights in grams (WW_g) using the length-weight relationship (Alex Wild, IATTC, La Jolla, unpubl. data for yellowfin tuna from the ETP)

$$FL = e^{((\ln(WW_g/1000)+11.184)/3.08612)},$$

The calibration growth curve for expected size-at-age in spotted dolphins was derived from equations and figures in Hohn and Hammond (1985) and unpublished data (A. Hohn, Southwest Fish. Sci. Cent., La Jolla). Weight-length conversions assumed the relationship

$$WW_{kg} = 1.4 * 10^{-5} * TL^{2.95},$$

where WW_{kg} is wet weight in kilograms, and TL is total length (tip of rostrum to fluke notch) in centimeters, based on weight-length measurements from a sample of 50 spotted dolphins ranging in size from 82 to 210 cm TL.

Equations Each model included equations for specific rates of consumption (C_{sp}), respiration (R_{sp}; including both swimming activity ACT_{sp}, and standard metabolism STD_{sp}), heat of digestion (specific dynamic action, SDA_{sp}), and waste losses (excretion plus egestion; WL_{sp}). Specific rate of growth is estimated simply as the difference between consumption and the sum of energy expenditures.

The form of the equation for each specific rate was the same for both models, with the exception of R_{sp}, which was estimated for yellowfin using Boggs' (1984) experimental results. R_{sp} was estimated for dolphins following Magnuson's (1978) procedure for estimating cost of swimming by carangiforms.

No effect of water temperature on consumption or respiration rates appears in either model. Ambient water temperature was assumed to be constant at 27°C, as most of the tuna-dolphin habitat occurs in waters of this temperature.

Consumption Specific rate of consumption (C_{sp}; calories food consumed · calories of animal^{-1} · day^{-1}) was estimated as

$$C_{sp} = CONS_{cal}/CAL_{an}$$

CAL_{an} is total caloric content of an individual yellowfin or spotted dolphin, estimated as a function of wet weight in grams,

$$CAL_{an} = CD * WW_g,$$

where CD is caloric density (cal/g wet wt) of yellowfin tuna[1] or spotted dolphins[2].

$CONS_{cal}$ is total calories consumed per individual per day, estimated as

$$CONS_{cal} = CONS_{ind} * CD_f,$$

where CD_f is caloric density of food (cal/g wet wt) for

[1] 1440 cal/g wet wt (Boggs 1984).

[2] CD_a = 1860 cal/g wet wt; average caloric density of four dolphins measuring 81–189 cm TL. Caloric density of each animal was determined as the sum of calories contained in blubber, muscle, viscera, and bone divided by total animal wet weight in grams. Average caloric density of individual dolphins ranged from 1985 cal/g wet wt in the 81 cm animal, to 1760 cal/g wet wt in the large adult female (189 cm TL). Assuming constant energy density for spotted dolphins is acceptable, as spotted dolphins do not appear to exhibit any significant seasonal, and little age-related, changes in thickness of their blubber layer.

yellowfin tuna[3] or spotted dolphins[4], and $CONS_{ind}$ is wet weight in grams of food consumed, estimated as

$$CONS_{ind} = C_{max} * P_{val} * WW_g,$$

where C_{max} is maximum possible consumption (expressed as a fraction of wet weight) for the largest yellowfin or dolphin, estimated as

$$C_{max} = C_a * WW_g^{Cb},$$

where [5]$C_a = 1.2$ and [6]$C_b = -0.22$ for yellowfin, or [7]$C_a = 3.98$ and [8]$C_b = -0.29$ for spotted dolphins.

P_{val} is an iteratively fitted unitless value in the range 0–1 that, when "correct," results in the simulated growth curve matching the observed growth curve (University of Wisconsin Sea Grant 1989), and WW_g is body wet weight in grams.

Respiration (yellowfin tuna) Specific rate of respiration (R_{sp}; calories respired · calories of animal^{-1} · day^{-1}) for yellowfin tuna was estimated as

$$R_{sp} = (STD_w + ACT_w) * (20650/CD),$$

with energy costs of standard (STD_w) and active (ACT_w) metabolism expressed in watts. The factor 20650 converts watts to cal/day. Dividing by caloric density of the animal (CD) produces the specific rate.

Weight-specific energy cost of standard metabolism for yellowfin was assumed constant for all sizes of yellowfin (Boggs 1984) as

$$STD_w = 0.464 \text{ watts/g wet weight.}$$

Energy cost of active metabolism (watts/g wet wt) was estimated using Boggs' (1984) equations and data for energy costs of activity in yellowfin,

$$ACT_w = F * VL^G * FL^H,$$

where VL is velocity in cm/sec and $F(=1.59\ E^{-4})$, $G(=1.64)$, and $H(=-1.28)$ are fitted parameters derived from Boggs' (1984) laboratory studies on yellowfin energetics.

Yellowfin were assumed to swim at length-specific optimum-sustained cruising speeds, with velocity scaling to fish length as

$$VL = VL_a * FL^{VLb},$$

where [9]$VL_a = 20.6$, and [10]$VL_b = 0.4$.

Respiration (spotted dolphins) Specific rate of respiration (R_{sp}; calories respired · calories of animal^{-1} · day^{-1}) for spotted dolphins was estimated as

$$R_{sp} = (ACT_{sp} + STD_{sp} + HL_{rsp}),$$

where ACT_{sp} is specific rate of swimming activity, STD_{sp} is specific rate of standard (basal) metabolism, and HL_{rsp} is specific rate of residual heat loss.

Specific rates of swimming activity and standard metabolism are estimated as

$$ACT_{sp} = ACT_{cal}/CAL_{an}$$

and

$$STD_{sp} = STD_{cal}/CAL_{an}.$$

Caloric cost of **standard metabolism** was estimated as

$$STD_{cal} = S_a * WW_g^{Sb},$$

[3] Energy density of yellowfin food was based on an assumed diet of 70% fish, 20% squid, and 10% invertebrates (Olson and Boggs 1986), with undigestible fractions of 0.124, 0.066, and 0.025, and caloric densities of 1440, 1260, and 1000 cal/g wet wt, respectively. Average ingested energy density (including the undigestible fraction) is 1380 cal/g wet wt.

[4] Energy density of spotted dolphin food changes with age (size). Spotted dolphins nurse throughout their first year (Perrin et al. 1976). They do not begin to ingest solid food until their second year, and they do not stop nursing entirely until their third year when they are ~145 cm in length. In this simulation, dolphins up to 1 yr of age were assumed to consume only milk (2855 cal/g wet wt) (Pilson and Walker 1970). Diet during the second year was assumed to be the same as that for yellowfin tunas, with an ingested energy density (CD_f) of 1380 cal/g wet wt.

[5] Based on the assumption that maximum specific feeding rate for very large yellowfin tunas (95000 g wet wt) would not exceed 10%/day, then solving for the intercept C_a (i.e., $C_a = 0.10/(95000^{-0.22})$) yields $C_a = 1.2$. In practice, the exact value chosen for C_{max} is flexible, as higher values simply reduce the fitted value of P_{val}, and vice versa.

[6] By analogy to walleye *Stizostedion vitreum* (Kitchell et al. 1977).

[7] Assuming maximum possible ration for adult spotted dolphins (~75 kg) would not exceed 15% of body weight/day (Sergeant 1969), and with $C_{max} = 0.15$, $WW_g = 85000$ g, and $C_b = -0.29$, then $C_a = 3.98$.

[8] As a compromise between the unresolved arguments of Kleiber (1961; $C_b = -0.25$) and Heusner (1982; $C_b = -0.33$) for scaling of metabolic rate with size in mammals. This compromise was chosen because consumption is not strictly a metabolic rate. While Huesner's argument for metabolic rate is supported by data for metabolic rate changes with size (see formulation for dolphin respiration), no such data exist for consumption rates.

[9] Intercept estimate based on 100 cm FL yellowfin swimming on average 130 cm/sec *in situ* (Holland et al. 1990).

[10] Slope estimate based on theoretical and empirical studies by Weihs (1973, 1981).

where $^{11}S_a = 1380$, and $^{12}S_b = 0.67$.

Caloric cost of activity[13] was estimated as

$$ACT_{cal} = PWR * 20650,$$

where 20650 converts watts to calories/day. Power required to swim (PWR) was estimated as

$$PWR = MP/(ME * PE),$$

where MP is mechanical power required to overcome drag, ME is mechanical efficiency,[14] and PE is "propeller efficiency" (efficiency of propulsion by flukes)[15]. MP (in watts) was estimated as a function of total drag (D_t; in dynes) and velocity (VL; in c/sec) as

$$MP = (D_t * L)/10^7,$$

where the factor 10^7 converts the product $D_t * L$ to watts.

Total drag was estimated as a function of drag due to body, fins, and movements by flukes as

$$D_t = (0.5 * N * VL^2 * S_w * C_t)/(1.0 - FID),$$

where N is density of seawater (1.025 g/cm^3), S_w is wetted surface area of the body, C_t is coefficient of total drag, and FID is (fin + induced) drag. FID[16] is expressed here as the fractional increase in estimated total drag due to adding the effects of fins and moving flukes.

S_w is wetted surface area of the body, excluding flippers, dorsal fin, and flukes, estimated as[17]

$$S_w = 0.1636 * TL^{2.14}.$$

Surface areas of fins are excluded from this calculation because fin drag is incorporated into the equation for total drag as an increase of 21% over drag estimated from body dimensions alone.

C_t was estimated from the formula for drag of submerged streamlined bodies moving with constant velocity

$$C_t = C_f * [1 + (1.5 * (D_a/TL)^{3/2}) + (7 * (D_a/TL)^3)]$$

(Hoerner 1965, Webb 1975). C_f is the coefficient of friction drag, and D_a is the maximum body diameter (cm; derived from girth at axilla (G_a)) where

$$G_a = G_{aa} * WW_{kg}^{Gab},$$

with $G_{aa} = 25$ and $G_{ab} = 0.28$, based on measurements of 50 spotted dolphins measuring 82–210 cm TL.

C_f was estimated from the equation for streamlined bodies moving submerged at constant velocity in turbulent flow as

$$C_f = 0.072\ R_L^{-1/5},$$

where R_L is Reynolds number, estimated here as

$$R_L = (TL * VL)/v,$$

where v is kinematic viscosity (= 0.01 Stokes) assuming turbulent flow at the boundary layer (Webb 1975), and VL is velocity (cm/sec), estimated as

$$VL = VL_a * TL^{VLb},$$

[11] Sa was assumed constant for all sizes of spotted dolphins. Given an observed rate of 0.45 mg $O_2 \cdot$ g wet wt$^{-1} \cdot$ hr^{-1} for a spinner dolphin *Stenella longirostris* weighing 68000 WW_g (Hampton and Whittow 1976) and assuming 3.25 cal/mg O_2 (Elliot and Davidson 1975), then 2,386,800 (0.45*3.25*68000) calories are expended daily in standard metabolism, and $S_a = 1380$ (2,386,800/68,000$^{0.67}$). The observed resting rate of oxygen consumption is consistent with the range of resting rates (0.3–0.6 mg $O_2 \cdot$ g wet wt^{-1}) reported for bottlenose dolphins under various conditions (Hampton et al. 1971, Karandeeva et al. 1973, Hampton and Whittow 1976).

[12] Heusner (1982) presents convincing statistical arguments that intraspecific relationships between basal (standard) metabolism and body weight in adult mammals are better described by the 2/3 power than the 3/4 power proposed by Kleiber (1961). Heusner's argument is based on observed differences between adults of similar species (e.g., breeds of dog); but Huesner's curve is also more realistic because it predicts a relatively higher weight-specific rate in smaller (younger) animals of a given species. This is more consistent with Kleiber's (1961) observation that younger animals tend to have elevated weight-specific metabolic rates compared not only with adults of the same species, but with small adults of similar species. In young marine mammals, weight-specific standard metabolic rate is often at least twice the standard rate of adults (Ashwell-Erickson and Elsner 1981, Lavigne et al. 1982). The parameterization above results in weight-specific estimates of S that are 2.3–1.3 times higher in dolphins measuring 80–140 cm TL than in adult dolphins (~190 cm TL). This differs by 0–11% (increasing with increasing size) from basal metabolic rates of juvenile through adult seals of similar weight (Ashwell-Erickson and Elsner 1981).

[13] Dolphins were assumed to swim steadily far enough below the surface to eliminate the effects of surface drag (e.g., Hertel 1969). This formulation ignores the costs of surfacing to breathe, and the attendant increase in total distance swum to follow a sinusoidal rather than a straight path through the water. Preliminary estimates of these additional costs for individual dolphins of several sizes, for reasonably realistic depths of dive and distance between surfacings, ranged from 10 to 25% of steady swimming costs. As this cost is relatively low, the dolphin model was not reformulated to include these added costs of surfacing.

[14] ME = 0.20, by analogy to observed muscle efficiencies of terrestrial mammals.

[15] PE = 0.85 by analogy to tunas (Magnuson 1978).

[16] FID was assumed = 0.21, based on the fraction of estimated total (body + fin + induced) drag accounted for by (fin + induced) drag in the 4-dolphin sample.

[17] Based on measurements of wetted surface area in the 34-dolphin sample.

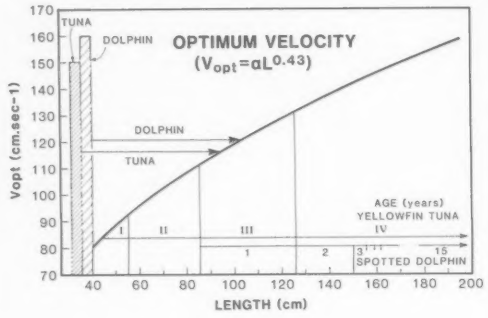


Figure 4

Estimated optimum sustained swimming speed (curved line) of yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata* from the eastern tropical Pacific Ocean. Lengths: fork length for tuna; rostrum to fluke notch ("total length") for dolphins. Vertical bars indicate range of optimum speeds predicted for sizes of tuna and dolphins occurring in mixed associations. Arrows indicate observed average swimming speeds of a radio-tagged 96 cm yellowfin tuna and of tagged individual spotted dolphins swimming *in situ*. Size-ranges for yellowfin tuna ages I–IV, and for spotted dolphins from birth, are indicated above abscissa.

where $VL_a = 20.6$ and $VL_b = 0.43$, assuming swimming velocity scales with length in the same manner for both spotted dolphins and yellowfin tuna (Fig. 4). Using the same formula and parameters to predict velocity as a function of length in both the tuna and dolphin models maintains comparability between results from the two models. As geometrically similar swimmers, hydrodynamic constraints should be approximately the same for both tuna and dolphins.

Specific rate of residual heat loss (HL_{rsp}; calories heat lost in excess of that generated by active and standard metabolism, and specific dynamic action · calories of animal^{-1} · day^{-1})[18] was estimated as

$$HL_{rsp} = HL_{usp} - (ACT_{sp} * (1.0 - ME) + STD_{sp} + SDA_{sp}),$$

where $HL_{rsp} > 0$, otherwise $HL_{rsp} = 0$.

The term (1.0 – ME) in conjunction with ACT_{sp} expresses the fraction of total active metabolism that is dissipated as heat, rather than converted to mechanical energy. The term H_{rsp} was taken to be zero when the estimate of H_{rsp} yielded a negative result. In this case, all passive losses were more than offset by heat generated by metabolism.

Specific rate of unavoidable passive heat loss (HL_{usp}; calories lost passively as heat · calories of animal^{-1} · day^{-1}) was estimated following Brodie's (1975) procedure for passive losses in large whales,

$$HL_{usp} = \frac{((21.18/BD_a) * (37.0 - T_a) * S_m/10000.0) * 24}{WW_g * (CD_d/1000.0)},$$

where [19]BD_a is average blubber depth, CD_d is caloric density of spotted dolphins, 37.0 (°C) is the assumed core temperature for spotted dolphins (Hampton and Whittow 1976), T_a is ambient temperature (assumed constant at 27°C), 21.18 is the conductivity factor for whale blubber (Brodie 1975), and [20]S_m is metabolic surface area, estimated as

$$S_m = 0.84 * S_w.$$

Unavoidable heat loss from fins and head is assumed negligible, as blood flow to these areas can be adjusted to minimize or maximize heat loss, as needed.

Specific dynamic action Specific rate of specific dynamic action (SDA_{sp}; calories lost as heat of digestion · calories of animal^{-1} · day^{-1}) was estimated as

$$SDA_{sp} = SDA * C_{sp},$$

where SDA (the fraction of consumption converted to heat energy during digestion) = 0.15 for both yellowfin tuna[21] and spotted dolphins[22].

Waste losses Specific rate of waste losses (WL_{sp}; calories lost as feces or urine · calories of animal^{-1} · day^{-1}) were estimated as the sum of fractional losses to egestion (F_a) and excretion (U_a)

[18] Because spotted dolphins are warm-blooded relative to their environment and because their blubber layer is not a perfect insulator, they will constantly lose heat to surrounding water. If the sum of estimated heat production generated by muscle activity, standard metabolism, and specific heat of digestion equals or exceeds this unavoidable passive loss, the term has no effect. Otherwise, the additional heat loss was added to the animal's energy cost. In practice, the influence of the term was negligible, as differences between H_d and the sum of STD, ACT, and SDA were <10%.

[19] BD_a = 0.65 cm, based on measurements of blubber depth at maximum girth for a sample of 72 spotted dolphins measuring 80–190 cm TL.

[20] S_m is the surface area of the body beneath the blubber layer. S_m averaged 84% of S_w in the 4-dolphin sample.

[21] Reflecting the relative high-protein low-carbohydrate diet ingested by yellowfin tunas (Olson and Boggs 1986).

[22] SDA is primarily a function of the protein content of ingested food, and is ~15% for a variety of carnivores, including sea otters eating clams and squid (10–13%, Costa and Kooyman 1984), harp seals eating fish (17%, Gallivan and Ronald 1981), and various terrestrial mammals fed a mixed diet (Kleiber 1961).

$$WL_{sp} = (F_a + U_a) * C_{sp},$$

where $^{23}F_a = 0.20$ and $^{24}U_a = 0.07$ for yellowfin tuna; $F_a = 0.125$ and $U_a = 0.07$ for spotted dolphins[25].

Growth Specific rate of growth (calories available for growth · calories of animal^{-1} · day^{-1}) was estimated as

$$G_{sp} = C_{sp} - (R_{sp} + SDA_{sp} + WL_{sp}).$$

Total calories available for growth (G_{cal}) is

$$G_{cal} = G_{sp} * CAL_{an}.$$

Total grams wet-weight biomass available for growth (G_{wwg}) is then

$$G_{wwg} = G_{cal}/CD.$$

The formulas and parameter values presented above produce reasonable model estimates of the various energy fluxes for both yellowfin tuna and spotted dolphins (Edwards 1992).

Results: Estimated consumption

Despite the apparent similarity between yellowfin tuna and spotted dolphins in food **composition** (prey type and size[26]), estimated food **requirements** for tuna and dolphins differ considerably. Estimated food requirements for individual tuna and dolphins imply that each dolphin requires 5–10 times more food per day than each yellowfin tuna, depending on the sizes of the tuna and dolphin being compared (Fig. 5). In a "typical" association of 200 dolphins and 500 tuna, total dolphin requirements are still 2–5 times higher than total tuna requirements per time-period (Fig. 6), despite the greater number of tuna than dolphins.

[23] Based on the relative assumed nondigestible portions of tuna diet items by analogy to similar items (Cummins and Wuycheck 1971).
[24] Based on measurement of non-fecal excretion by carnivorous fish (Brett and Groves 1979).
[25] Together these processes probably account for 15–20% of ingested food energy in spotted dolphins, as found for other small marine mammals eating fish (Shapunov 1973, Ronald et al. 1984, Ashwell-Erickson and Elsner 1981, Lavigne et al. 1982, and references therein.)
[26] Diet is undoubtedly an important factor in the tuna-dolphin association, as associated yellowfin tuna and spotted dolphins apparently have nearly identical feeding preferences (Perrin et al. 1973). Stomach contents of co-occurring tuna and spotted dolphins consisted primarily of small pelagic schooling fish (e.g., mackerel *Auxis thazard*) and squid of similar types and sizes.

Discussion: Model implications

The strict "result" of exercising the models is estimation of food consumption by yellowfin tuna and spotted dolphins of various sizes. This information alone is not particularly helpful in furthering our understanding of the tuna-dolphin bond. However, the process of model

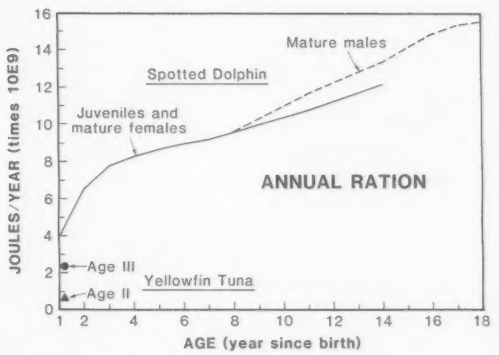


Figure 5
Estimated annual ration for individual spotted dolphins *Stenella attenuata* ages birth–18 yr, and yellowfin tuna *Thunnus albacares* ages II–III, occurring in mixed associations in the eastern tropical Pacific Ocean.

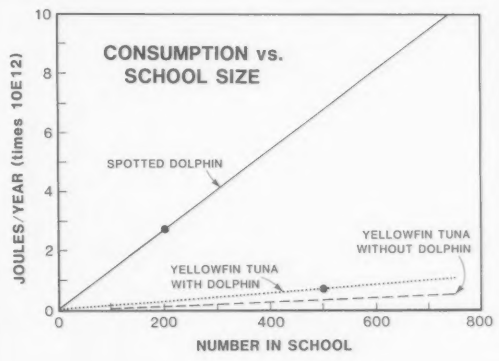


Figure 6
Estimated annual ration for schools of yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata* occurring in mixed associations in the eastern tropical Pacific Ocean (ETP). Solid circles indicate number of individual dolphins and individual tuna in a typical mixed association. Ration estimates for schools were based on average observed size-frequency distributions of tuna and dolphin in the ETP.

development and comparisons of similar energy fluxes in the completed models generated several interesting observations with potentially significant implications.

Hydrodynamics and body length

Length frequencies of the tuna and dolphins in a typical association show a surprisingly strong overlap between age-III yellowfin and neonate–1st yr dolphins. Both animals begin their respective years at ~85 cm TL, and complete the year at ~125 cm TL (Fig. 4). This is significant for two reasons. First, this size range comprises the majority of the yellowfin tuna found associated with dolphins (Fig. 3)[27]. Second, both animals have relatively stiff torpedo-shaped bodies with stiff fins and carangiform swimming behavior. Because theory predicts that optimum swimming speeds (the speed at which the least energy is consumed for a given distance covered) of geometrically-similar swimmers will be comparable (Weihs 1973, Webb 1975), the similar body forms and swimming behaviors of the tuna and the dolphins imply that optimum swimming speeds will also be similar for either animal of a given length.

Swimming speeds of sonic-tagged yellowfin tuna measured *in situ* show that individual undisturbed yellowfin, of the size most often found associated with dolphins, choose in their natural environment to swim on average at their predicted optimum cruising speed (e.g., yellowfin 90–100 cm FL swim at 100–130 cm/sec; Holland et al. 1990). Because yellowfin tuna tend to associate in schools of like-sized individuals, the expected speed of the tuna group is similar to the expected speed of the individuals involved.

In contrast, tracking studies (Perrin et al. 1979) of spotted dolphins in the ETP indicate that dolphin schools swim on average not the speed most efficient for the majority of the individuals in the school (i.e., ~160–170 cm/sec for large adults) but the speed most efficient for the neonate–1st yr animals (~120 cm/sec; Fig. 4).

These observations imply that yellowfin associating with dolphin schools may do so at little or no added hydrodynamic cost. The associated fish, unlike larger or smaller sizes of yellowfin, need swim neither faster nor slower than their apparently preferred optimum in order to maintain an association with dolphins.

The observation that associating with dolphins may cost tuna little does not explain **why** the tuna participate. The similarity in feeding preferences and probable similarity in feeding behaviors provides one explanation and suggests that tuna are more likely to follow dolphins than the reverse.

Who follows whom

The higher forage requirements of dolphins both individually and as an association imply that dolphins following tuna, particularly single dolphin schools following single tuna schools, would fall far short of meeting their daily energy requirements. Dolphin schools might avoid this energy deficit by switching from one tuna school to another, but they would have to switch consistently from recently-successful to soon-to-be-successful schools of foraging tuna. This frequent switching could be difficult because it would likely involve periods of searching at speeds greater than sustainable by the young dolphins, in order to find new tuna schools (and new patches of forage) faster than the patches could be found by the current tuna school.

Measurements of muscle mass and estimates of power-time curves for various sizes of spotted dolphins imply that the relatively small muscle mass of neonate–1st yr dolphins probably cannot sustain speeds much faster than their predicted optimum for any extended length of time (unpubl. data). If searching for new schools of tuna requires sustained accelerated swimming, the young dolphins could have trouble keeping up with the rest of the school. Because it is unlikely that dolphins, as nursing mammals and highly social animals, would simply leave their young behind, switching frequently from one tuna school to another may not be a practical option.

The disparity in feeding requirements implies that, while dolphins would probably be disadvantaged by having to rely upon tuna to locate sufficient prey, the tuna could recognize an advantage by following dolphins. The fish would then be associating with another predator that is searching for the same prey, but which must encounter that prey either more often or in considerably larger patches than required by the tuna, per time period.

However, the greater need of the dolphins for food implies concomitantly that competition for resources, if those resources are limited, could be fierce. The schooling characteristics of the predators and prey, coupled with feeding behaviors and differing sizes of the predators, provide one possible explanation for the ability of the smaller yellowfin tuna under some circumstances to persist in this potentially competitive association despite the dolphin's greater size, and need for food.

[27] Figure 3 includes fish from all areas of the fishery, not just the offshore areas where most dolphin fishing occurred during the years these data were collected, causing dolphin-fish distribution to be skewed to left.

WHEN SHOULD TUNA ASSOCIATE WITH DOLPHIN?

PREY ABUNDANCE:	LOW		HIGH	
PATCH TYPE:	RARE LARGE	FREQUENT SMALL	RARE LARGE	FREQUENT SMALL
ABILITY TO LOCATE PREY:				
D>T	YES	NO	YES	NO
D=T	NO	NO	NO	NO
D<T	NO	NO	NO	NO

Figure 7

Decision table predicting conditions under which yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata* should (or should not) associate.

Avoiding competition for food

As is characteristic of pelagic ocean systems, both predators and prey in the ETP occur in clumped distributions. Individuals occur in schools or aggregations separated by (often vast) distances devoid of other individuals. The prey, like the yellowfin tuna, will tend to occur in schools of like-sized individuals with similar swimming speeds. Aggregations of tuna and dolphins will typically consist of dolphins of assorted sizes accompanied by tuna of approximately one size. The feeding strategy of the predators will involve searching for a clump of prey, simultaneous (or nearly so) arrival at the prey patch by both tuna and dolphins, and repeated incursions by individuals of both predator groups into the clump of prey wherein prey are seized and swallowed whole individually.

Associated yellowfin tuna may be able to mitigate this direct competition with dolphins for food on the basis of the difference in size between the fish and the feeding adult dolphins (~100 cm vs. 200 cm TL). Because the tuna are smaller, they have smaller maximum stomach capacity (~400 g wet wt for age-2 yellowfin, ~1100 g wet wt for age-3 yellowfin; Olson and Boggs 1986) compared with spotted dolphins (~2000 g wet wt in adults; Bernard and Hohn 1989). Even if the smaller, presumably more-agile tuna could seize individual prey only as fast as the dolphins and no faster, they would satiate more quickly than the dolphins.

As both groups would begin feeding at the same time, when the prey concentration was maximum, the tuna at any time would be relatively closer than the dolphins to satiation, given the observed (average) relative proportions of tunas and dolphins in a typical association. The tuna would be filling their stomachs while the prey were still relatively dense. Depending on the size of the prey patch, dolphins might never succeed in satiating, even though the tuna had their fill. Even if the prey patch was sufficiently limited that neither group achieved satiation, the tuna would always be relatively more full at any given time. Thus, although the dolphins require more prey overall, the tuna could succeed competitively by satiating sooner (being relatively more successful) during any given prey encounter.

However, it may not always be to the tuna's advantage to associate with dolphins, even given this scenario. The benefit (or not) can be assessed by evaluating the relative advantages of associating or not, given the range of possibilities for prey spatial distribution and abundance.

When should the association occur?

The possibilities can be summarized in a simple decision table (Figure 7). At the extremes, prey abundance may be either low or high and any given abundance may be either homogeneously distributed (frequent) or clumped (rare). The possibilities for locating prey are that (1) dolphins are more adept than tuna, (2) both are equally adept, or (3) dolphins are less adept than tuna. The advantages for tuna to associate with dolphins can be assessed for each cell in the table.

Consideration of each cell in the table suggests that tuna may benefit from associating with dolphins only when (1) prey are distributed in rare patches and (2) dolphins are more adept than the tuna in finding these patches. This would be true regardless of prey concentration within the patches, because whenever tuna and dolphin associate they will compete for food. If tuna are more adept than dolphins at finding food, then there will be no foraging-related advantage for the tuna to associate with their competitors. The tuna would be able to find food more easily on their own than by following dolphins, and would not have to risk sharing these resources once located. If the tuna and dolphins are equally adept, there is still no advantage, for the same reason.

If the prey are distributed in relatively small but numerous patches, there is still no advantage for tuna to associate with dolphins, again because the spatial frequency of schools would produce a relatively high probability of tuna encountering the food on their own without risk of sharing with their competitor. In addition, when patches are small, the tuna would be especially disadvantaged by having to compete with dolphins because the presence of dolphins could prevent the tuna from satiating, despite the fact that the tuna would still be relatively more full than the dolphins when the patch had been exhausted.

But when the prey are distributed in rare patches **and** the dolphins are more adept than the tuna at locating these patches, then tuna could benefit from associating with dolphins because the fish could encounter food more often than if they were not associated. This will be true regardless of the density of the prey patch.

It is never the case that dolphins benefit energetically from depending entirely on tuna for finding prey, because dolphin forage requirements are so much higher than tuna requirements.

These conclusions lead to the hypothesis that tuna-dolphin associations should be more prevalent in areas where oceanic conditions encourage strong clumping of prey, and less prevalent when conditions encourage a more homogeneous distribution of prey. I am currently exploring, with a simulation model of tuna, the movements of dolphin and prey in response to environmental characteristics of the ETP (work in progress). Further studies correlating oceanic environmental characteristics with catches of various size-classes of tuna are planned but not yet underway. If the suggestions described above are borne out, it may be possible to identify areas of the ETP where large yellowfin tuna could be captured without having to rely on dolphin-associated fishing.

Caveats

This study assumes that average size of dolphin schools remains constant at about 200 animals. This is the average school size for spotted dolphins observed during dolphin survey research cruises in the ETP. In fact, neither school size nor school composition are constant. Observers on both research and commercial vessels report school sizes ranging from a few animals to many hundreds. Scott (1991) reports diel changes in sizes of schools sighted by tuna fishermen in the ETP.

However, these inconsistencies may not significantly affect the implications of the energetics estimates presented here. Average sizes of dolphin schools captured with tuna in the ETP are considerably larger (400–600 animals) than the average school size observed during research surveys because the fishermen preferentially search and capture large schools of dolphins, which tend to carry more tuna. Estimates concerning the relative importance of tuna and dolphins to energetics of the association are probably reasonably similar for both large and small associations, because in both cases the proportions of tuna and dolphins tend to be similar (i.e., as the number of dolphins increases, in general the number of associated tuna increases). The study of diel differences (Scott 1991) shows that school sizes of dolphins sighted in association with tuna vary from a morning low to a late-afternoon high, but the change is relatively small, from ~450 to ~600 animals on average.

Other explanations for the bond

Other hypotheses have been proposed to explain the tuna-dolphin association. The two most-often suggested are the possibility that tuna perceive dolphin schools as FADs (fish aggregating devices) or as protection from sharks. Both of these factors may well contribute to the strength of the bond; neither precludes the energetics results discussed above.

The propensity for fish to collect around floating objects is well known, although the reasons are not yet understood. Presumably, floating objects provide a reference point for the aggregating tuna and in some way increase foraging success, perhaps by concentrating prey items or by tracking convergence areas where prey densities may be higher than elsewhere.

The FAD hypothesis has merit for the sizes of tuna actually found with dolphins in the ETP, for two reasons in particular. First, associating with dolphins may increase foraging success for the associated tuna because both tuna and dolphins are apparently seeking the same prey and dolphins may be more adept at finding it. Thus, tuna are associating with a FAD that does not simply attract appropriate prey passively, but actively searches and finds it. Second, tuna are required to swim constantly in order to ventilate their gills. It appears convenient that the average observed speed of dolphin schools is also the optimum speed of the sizes of tuna usually found associated with these schools. Rather than circling a stationary FAD, tuna associated with dolphin schools will cover a much larger area while moving at their most efficient cruising speed, and will cover that area in the presence of a sentient foraging FAD.

The shark protection hypothesis derives from a common perception that dolphins actively protect their young by driving sharks from their vicinity. If this is so, tuna associating with dolphins may be associating with the best of all possible FADs; a floating object that moves at the tuna's optimal speed, moves in search of the same prey the tuna would like to find, is probably at least as adept as the tuna at finding that preferred prey, and which provides protection against, rather than increased risk of, predation (FADs of course concentrate not only fish, but also their predators).

Both the FAD and shark hypotheses assume that tuna follow dolphins. Not all hypotheses assume that tuna are the followers. Au and Pitman (1986) and Au (1991) suggest, for example, that dolphins follow tuna in order to take advantage of tuna foraging in conjunction with bird flocks. This would be an advantage for dolphins during the actual feeding event. However, it

does not solve the problem that dolphins apparently must locate not only the same type of prey as large yellowfin tuna, but quite a bit more of it during any given time-period. Following tuna does not appear adequate to fulfill dolphin schools' energy requirements.

This fundamental difference in food energy requirements may be the single most important **biological** factor underlying the association. Oceanographic conditions (the shallow mixed layer) set the stage; energetics requirements (hydrodynamics and foraging patterns) appear to constrain the roles. Although the definitive answer has yet to be demonstrated quantitatively, the energetics-based hypotheses presented here are at least consistent with currently available data. The tuna-dolphin association may be a consequence of a combination of oceanography, hydrodynamics, foraging energetics, and life-history characteristics, i.e, a consequence of the ecology of the association's components.

Acknowledgments

This study could not have been completed without generous sharing of data, time, and constructive advice by helpful individuals from, but not limited to, the National Marine Fisheries Service, Southwest Fisheries Science Center, and the Inter-American Tropical Tuna Commission. This work was completed while the author was a National Research Council PostDoctoral Research Associate at the Southwest Fisheries Science Center, La Jolla, CA.

Citations

Ashwell-Erickson, S., and R. Elsner
1981 The energy cost of free existence for Bering Sea harbor and spotted seals. *In* Hood, D.W., and J.A. Calder (eds.), The eastern Bering Shelf: Oceanography and resources, vol. 2, p. 869–899. Univ. Wash. Press, Seattle.

Au, D.W.
1991 Polyspecific nature of tuna schools: Shark, dolphin, and seabird associates. Fish. Bull., U.S. 89:343–354.

Au, D.W.K., and R.L Pitman
1986 Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Condor 88(3):304–317.

Barlow, J., and A. Hohn
1984 Interpreting spotted dolphin age distribution. NOAA-TM-NMFS-SWFC-48, Southwest Fish. Sci. Cent., La Jolla, 21 p.

Bernard, H.J., and A.A. Hohn
1989 Difference in feeding habits between pregnant and lactating spotted dolphins (*Stenella attenuata*). J. Mammal. 70(1):211–215.

Boggs, C.H.
1984 Tuna bioenergetics and hydrodynamics. Diss. Abstr. Int. 45/02-B:482.

Brett, J.R., and D.D. Groves
1979 Physiological energetics. *In* Hoar, W.S., et al. (eds.), Fish physiology, vol. 8, p. 280–354. Academic Press, NY.

Brodie, P.F.
1975 Cetacean energetics, an overview of intraspecific size variations. Ecology 56:152–161.

Costa, D.P., and G.L. Kooyman
1984 Contribution of specific dynamic action to heat balance and thermoregulation in the sea otter, *Enhydra lutris*. Physiol. Zool. 57(2):199–203.

Cummins, K.W., and J.W. Wuycheck
1971 Caloric equivalents for investigations of ecological energetics. Int. Assoc. Theor. Appl. Limnol. Proc. 18:1–158.

Edwards, E.F.
1992 Evaluation of energetics models for yellowfin tuna (*Thunnus albacares*) and spotted dolphin (*Stenella attenuata*) in the eastern tropical Pacific Ocean. Admin. Rep. LJ-92-01, NMFS Southwest Fish. Sci. Cent., La Jolla, 43 p.

Elliot, J.M., and W. Davidson
1975 Energy equivalents of oxygen consumption in animal energetics. Oecologia (Heidelb.) 19:195–120.

Fiedler, P.C.
1990 Seasonal climatologies and variability of eastern tropical Pacific surface waters. NOAA Tech. Rep. NMFS 109, 65 p.

Fiedler, P.C., L.J. Lierheimer, S.B. Reilly, S.N. Sexton, R.S. Holt, and D.P. DeMaster
1990 Atlas of eastern tropical Pacific oceanographic variability and cetacean sightings, 1986–1989. NOAA-TM-NMFS-SWFSC-144, Southwest Fish. Sci. Cent., La Jolla, 142 p.

Gallivan G.J., and K. Ronald
1981 Apparent specific dynamic action in the harp seal (*Phoca groenlandica*). Comp. Biochem. Physiol. 69A:579–581.

Hampton, I.F.G., and G.C. Whittow
1976 Body temperature and heat exchange in the Hawaiian spinner dolphin *Stenella longirostris*. Comp. Biochem. Physiol. 55A:195–197.

Hampton, I.F.G., G.C. Whittow, J. Szekerczes, and S. Rutherford
1971 Heat transfer and body temperature in the Atlantic bottlenose dolphin, *Tursiops truncatus*. Int. J. Biometrics 15(2–4):247–253.

Hertel, H.
1969 Hydrodynamics of swimming and wave-riding dolphins. *In* Anderson, H.T. (ed.), Biology of marine mammals, p. 31–63. Academic Press, NY.

Heusner, A.A.
1982 Energy metabolism and body size. Part I. Is the 0.75 mass exponent of Kleiber's equation a statistical artifact? Respir. Physiol. 48:1–12.

Hoerner, S.F.
1965 Fluid dynamic drag: Practical information on aerodynamic drag and hydrodynamic resistance. Published by author, Midland Park, NJ, 468 p.

Hohn, A.A., and P.S. Hammond
1985 Early postnatal growth of the spotted dolphin in the offshore eastern tropical Pacific. Fish. Bull., U.S. 83:533–556.

Holland, K.M., R.W. Brill, and R.K.C. Chang
1990 Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. Fish. Bull., U.S. 88:493–507.

IATTC (Inter-American Tropical Tuna Commission)
1989 Annual report, 1988. Inter-Am. Trop. Tuna Comm., Scripps Inst. Oceanogr., La Jolla, 288 p.

Joseph, J.
1963 Fecundity of yellowfin tuna (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) from the eastern Pacific Ocean. Int.-Am. Trop. Tuna Comm. 7(4):257–292.

Karandeeva, O.G., S.K. Matisheva, and V.M. Shapunov
1973 Features of external respiration in the Delphinidae. *In* Chapskii, K.K., and V.E. Salokov (eds.), Morphology and ecology of marine mammals, p. 196--206. John Wiley, NY.

Kessler, W.S.
1990 Observations of Long Rossby Waves in the northern tropical Pacific. J. Geophys. Res. 95(C4):5183–5217.

Kitchell, J.F., D.J. Stewart, and D. Weininger
1977 Application of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board. Can. 34:1922–1935.

Kleiber, M.
1961 The fire of life. John Wiley, NY, 453 p.

Lavigne, D.M., W. Barcyard, S. Innes, and N.A. Oritsland
1982 Pinniped bioenergetics. *In* Mammals in the sea, vol. 4, p. 192–235. FAO Fish. Ser. 5.

Magnuson, J.J.
1978 Locomotion by scombrid fishes: Hydrodynamics, morphology and behavior. *In* Hoar, W.S., et al. (eds.), Fish physiology, vol. 7, p. 239–313. Academic Press, NY.

Olson, R.J., and C.H. Boggs
1986 Apex predation by yellowfin tuna (*Thunnus albacares*): Independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. Can. J. Fish. Aquat. Sci. 43(9):1760–1775.

Orbach, M.
1977 Hunters, seamen and entrepreneurs. The tuna seinermen of San Diego. Univ. Calif. Press, Berkeley, 304 p.

Perrin, W.F.
1969 Using porpoises to catch tuna. World Fishing 18(6), 4 p.

Perrin, W.F., R.W. Warner, C.L. Fiscus, and D.B. Holts
1973 Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., U.S. 71:1077–1092.

Perrin, W.F., J.M. Coe, and J.R. Zweifel
1976 Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229–269.

Perrin, W.F., W.E. Evans, and D.B. Holts
1979 Movement of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969–1976. NOAA Tech. Rep. NMFS-SSRF-737, 14 p.

Pilson, M.E.Q., and D.W. Walker
1970 Composition of milk from spotted and spinner dolphins. J. Mammal. 51(1):74–79.

Ronald, K., K.M. Keiver, F.W.H. Beamish, and R. Frank
1984 Energy requirements for maintenance and faecal and urinary losses of the grey seal (*Halichoerus grypus*). Can. J. Zool. 62:1101–1105.

Scott, M.
1991 The size and structure of pelagic dolphin herds. Ph.D. thesis, Univ. Calif, Los Angeles, 165 p.

Sergeant, D.E.
1969 Feeding rates in cetacea. Fiskeridir. Skr. Ser. Havunders. 15:246–258.

Shapunov, V.M.
1973 Food requirements and energy balance in the black sea bottlenose dolphin (*Tursiops truncatus ponticus barabasch*). *In* Chapskii, K.K., and V.E. Solokov (eds.), Morphology and ecology of marine mammals, p. 207–212. John Wiley, NY.

Smith, T.D. (editor)
1979 Report of the status of porpoise stocks workshop, Aug. 27–31, La Jolla, CA. Admin. Rep. LJ-79-41, NMFS Southwest Fish. Sci. Cent., La Jolla, 138 p.

University of Wisconsin Sea Grant
1989 A generalized bioenergetics model of fish growth for microcomputers. WIS-SG-87-245, Univ. Wisc., Madison, 47 p.

Webb, P.W.
1975 Hydrodynamics and energetics of fish propulsion. Fish. Res. Board Can. Bull. 190, 159 p.

Weihs, D.
1973 Optimal fish cruising speed. Nature (Lond.) 245:48–50.
1981 Voluntary swimming of speeds of two species of large carcharhinid sharks. Copeia 1:219–222.

Wild, A.
1986 Growth of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean based on otolith increments. Int.-Am. Trop. Tuna Comm. Bull. 18(6), 56 p.

Wyrtki, K.
1966 Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Annu. Rev. 4:33–68.
1967 Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1(2):117–147.

Artificial shelters and survival of juvenile Caribbean spiny lobster *Panulirus argus*: Spatial, habitat, and lobster size effects*

David B. Eggleston

The College of William and Mary, Virginia Institute of Marine Science
Gloucester Point, Virginia 23062
Caribbean Marine Research Center, Lee Stocking Island, Exuma Cays, Bahamas
Present address: College of Ocean and Fishery Sciences WH-10
University of Washington, Seattle, Washington 98195

Romuald N. Lipcius

The College of William and Mary, Virginia Institute of Marine Science
Gloucester Point, Virginia 23062
Caribbean Marine Research Center, Lee Stocking Island, Exuma Cays, Bahamas

David L. Miller

Department of Geography, State University of New York, Cortland, New York 13045

Abstract.– A principal mechanism underlying a production hypothesis that artifical reefs increase environmental carrying capacity and eventually the biomass of reef-associated organisms is that these structures reduce predation on reef residents. We tested this predation mechanism with a series of field experiments at two sites (inner-bay sand-seagrass flat, and outer-bay seagrass bed adjacent to coral reefs) in Bahia de la Ascension, Mexico. We examined survival of two size-classes of juvenile Caribbean spiny lobster *Panulirus argus* tethered in seagrass beds with and without access to artificial lobster shelters, and at different distances from the shelters. The artificial shelters were concrete structures (casitas) that simulate lobster dens. Large juvenile lobsters (56–65 mm CL) attained a relative size refuge when tethered 60 m away from casitas compared with smaller (46–55 mm CL) lobsters. Conversely, the small lobsters survived better beneath casitas than did large lobsters. Small juveniles also survived better at casitas or 30 m away from casitas than at 15 m or 70 m away. Observations indicated that the daytime predator guild, composed primarily of snappers (family Lutjanidae), seldom foraged more than 60 m from casitas and were typically within 15 m of casitas. There was also a significant positive correlation between predation-induced lobster mortality and numbers of snapper associated with casitas at the inner-bay site. Thus, tethering lobsters 70 m away from casitas appeared adequate to examine survival of lobsters in an environment uninfluenced by daytime predators aggregating to casitas. These results indicate that (1) the relative importance of a lobster-size refuge from predators varies according to shelter availability, and (2) that there is a nonlinear relationship between predation risk and distance from an artifical shelter. Our results demonstrate that casitas increase survival of small juvenile lobsters but reduce survival of larger juveniles. Small casitas scaled according to body size may enhance survival of large juvenile lobsters in nursery habitats where large conspecifics are removed from large casitas.

Manuscript accepted 13 July 1992.
Fishery Bulletin, U.S. 90:691–702 (1992).

Artificial reefs are in use worldwide as a means of increasing local abundance of finfish and invertebrates (see reviews by Bohnsack and Sutherland 1985, Grove and Sonu 1985, Mottet 1985, Bohnsack 1989). The use of artificial reefs to increase fisheries production remains controversial because it is unknown whether these structures (1) provide critical resources that increase the environmental carrying capacity and eventually the biomass of reef-associated organisms (production hypothesis), or (2) merely attract and aggregate organisms from surrounding areas without increasing total biomass (attraction hypothesis) (Bohnsack 1989). The attraction hypothesis is an important consideration for artificial-reef-based fisheries that may be vulnerable to overexploitation. Thus, there is a need for ecological investigations capable of assessing the impact of artificial reefs upon species distribution, abundance, and survival patterns, and the processes underlying these patterns.

Artificial reef technology has traditionally been based on the assumption that obligate reef dwellers (e.g., reef fishes and lobsters) are limited locally or regionally by the availability of shelter (Bohnsack 1989, Hixon and Beets 1989, Eggleston et al. 1990 and references therein). Conversely, artificial reefs also concentrate numerous potential predators (Hixon and Beets 1989, Eggleston et al. 1990); increased predation pressure at or near these structures could outweigh the benefits from increases in production. For instance, fishes and lobsters normally dispersed over a wide area could be concentrated and consumed by predators more rapidly in a smaller area. Thus, artificial shelters may either enhance or reduce the survival of their inhabitants, depending upon predator responses. In this paper, we present the results of a series of field experiments comparing survival rates of two size-classes of juvenile Caribbean spiny lobster *Panulirus argus*

*Contribution 1725 of the Virginia Institute of Marine Science.

Latreille, with and without access to artificial shelters at different spatial scales in seagrass beds. We then discuss these mortality patterns in terms of the relative importance of lobster size, shelter availability, and distance of lobsters from the artifical shelter. Moreover, we use daytime abundance and foraging ranges of shelter-associated predators to speculate on the mechanisms underlying these mortality patterns.

Juvenile *P. argus* inhabit shallow bays throughout the tropical and subtropical western Atlantic where they frequently aggregate during the day in crevices of coral and rocky reefs (Berrill 1975, Herrnkind et al. 1975). Gregarious behavior within dens probably enhances individual survivorship because spiny lobsters collectively use their spinose antennae to fend off diurnally active predators (Berrill 1975, Cobb 1981, Zimmer-Faust and Spanier 1987, Eggleston and Lipcius 1992). However, intra- and interspecific competition for suitable dens can force smaller juvenile *P. argus* out of these dens (Berrill 1975). Predation represents a major source of mortality for juvenile spiny lobsters (Munro 1974, Herrnkind and Butler 1986, Howard 1988, Smith and Herrnkind 1992), and when individuals are displaced or forced to shelter in an inadequate den they may be subject to increased predation rates (Herrnkind and Butler 1986, Eggleston et al. 1990).

Large juvenile and adult spiny lobsters are the focus of intense commercial and recreational fisheries in south Florida and the Caribbean, with the possibility of regional overexploitation of spiny lobster fisheries (U.S. Agency for International Development 1987). Several Caribbean nations have met increased market demand with the large-scale use of artificial shelters to concentrate lobsters and facilitate harvest (e.g., Mexico—Miller 1989, Lozano-Alvarez et al. 1991; Cuba—Cruz and Brito 1986; Bahamas—R.W. Thompson, Dep. Fish., Nassau, Bahamas, pers. commun., May 1991). These artificial shelters, commonly referred to as "casitas Cubanas" (see Fig. 1), attract and concentrate a broad size-spectrum of juvenile *P. argus*, particularly in nursery areas (Eggleston et al. 1990, Lozano-Alvarez et al. 1991).

Predation intensity in and around artificial shelters is affected by numerous factors including the sizes of predator, prey, and shelter (Hixon and Beets 1989, Eggleston et al. 1990), and distance from the reef (Shulman 1985). Moreover, since most crustaceans have indeterminate growth (Hartnoll 1982), they must continually search for larger shelters as they grow, a process that involves predation risk that is inversely related to body size (e.g., Scully 1983, Reaka 1987, Vermeij 1987). Hence, we hypothesized that (1) the relative importance of a lobster size refuge would vary according to shelter availability, and (2) that the impact of artificial shelters upon predation-induced mortality of juvenile lobsters would vary according to the distance of unprotected lobsters from these shelters. We tested these hypotheses experimentally in the field by quantifying the survival of tethered spiny lobster juveniles in seagrass beds of Bahia de la Ascension, Mexico. This bay is a productive nursery for juvenile *Panulirus argus* and supports a commercial fishery for large juveniles and adults (Miller 1989, Lozano-Alvarez et al. 1991). Experimental factors included (1) presence or absence of artificial shelter, i.e., casitas Cubanas, (2) lobster size, (3) site, and (4) distance between tethered, unprotected lobsters and artificial shelters.

Methods and materials

Study site

Tethering experiments were conducted in Bahia de la Ascension, a large bay (~740 km^2) within the Sian Ka'an Biosphere Reserve, Mexico (19°45′N, 87°29′W) (Fig. 2). Two experimental sites with contrasting

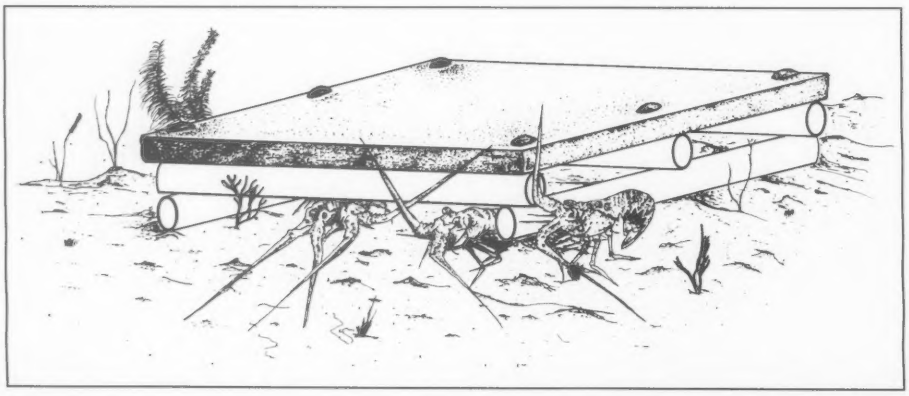


Figure 1
A large "casita Cubana" constructed with a frame of PVC-pipe and roof of cement (177 cm length × 118 cm width × 6 cm height of opening).

habitats were chosen to compare relative rates of predation: an inner-bay sand-seagrass (*Thalassia testudinum*) flat located at the northwestern portion of the bay, and an outer-bay seagrass meadow adjacent to a coral reef (Fig. 2). Seagrass and algal habitats likely provide the only natural daytime refuge for juvenile *P. argus* in this system because of an apparent lack of crevices (formed by rocky outcrops, patch coral reefs, sponges, solution holes, or undercut seagrass banks). Anecdotal information from lobster fishermen present in Bahia de la Ascension prior to the introduction of casitas (around 1974) indicated that juvenile lobsters commonly resided solitarily under dense stands of *Thalassia* or complex red algae (e.g., *Laurencia*), or aggregated around existing structures such as sponges or cobble. Moreover, previous tethering experiments with juvenile *P. argus* in this system demonstrated that seagrass and algae provide some protection for spiny lobster juveniles from predators (R.N. Lipcius et al., unpubl. data).

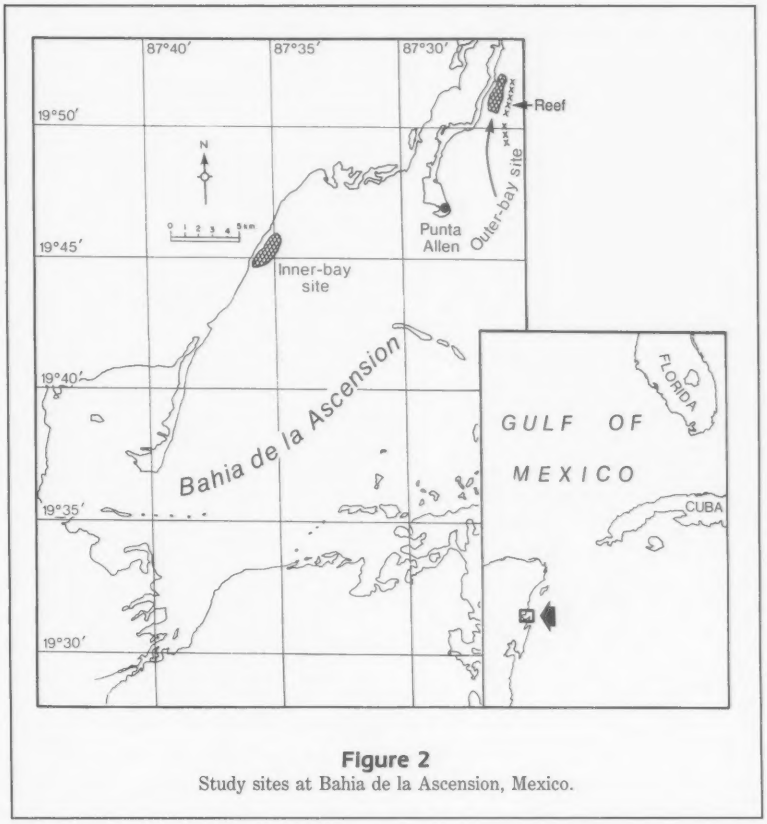


Figure 2
Study sites at Bahia de la Ascension, Mexico.

Differences in seagrass density between and within sites were determined prior to experiments by measuring dry-weight biomass (g) of *Thalassia* removed from 0.25 m^2 plots. The inner-bay site was composed of sparse seagrass patches ($\bar{x}$ *Thalassia* biomass 62.4 g/m^2, N 6, SD 10.7) interspersed among coarse calcareous sand and coral rubble. The coral rubble was covered mostly by green and red algae (*Dasycladus* spp. and *Laurencia* spp., respectively), but also supported larger sponges. The outer-bay site was located shoreward of a fringing coral reef and composed of sand patches and patch corals interspersed among moderate to dense seagrass beds ($\bar{x}$ *Thalassia* biomass 111.6 g/m^2, N 6, SD 13.4, and 210.0 g/m^2, N 6, SD 12.6, respectively). Further details of the study site are described in Eggleston et al. (1990).

Artificial shelters

Our design of artificial lobster shelters was based on "casitas Cubanas"—sunken wood and concrete structures that simulate lobster dens (Miller 1989) (Fig. 1). The large casitas used in this study (177x118x6 cm) were constructed with a reinforced concrete roof bolted to a supporting PVC-pipe frame. Several physical properties of the casita appear to make it an optimal lobster den: (1) shaded cover provided by the wide concrete roof, (2) a low ceiling that excludes large piscine predators, and (3) multiple den openings which are smaller than the inner roof height of the casita (Fig. 1) (Eggleston et al. 1990). Hence, the use of casitas permitted us to standardize den size and availability in different habitats.

Tethering experiments and predator observations

Spiny lobsters were collected from existing casitas and held in traps for 1–2 days prior to initiation of each experiment. Only intermolt lobsters exhibiting strong "tail flipping" responses were used in tethering experiments. Tethers were constructed by locking a plastic cable-tie around the cephalothorax of a lobster, between the second and third walking legs, and securing the cable-tie with cyanoacrylate cement. The cyano-

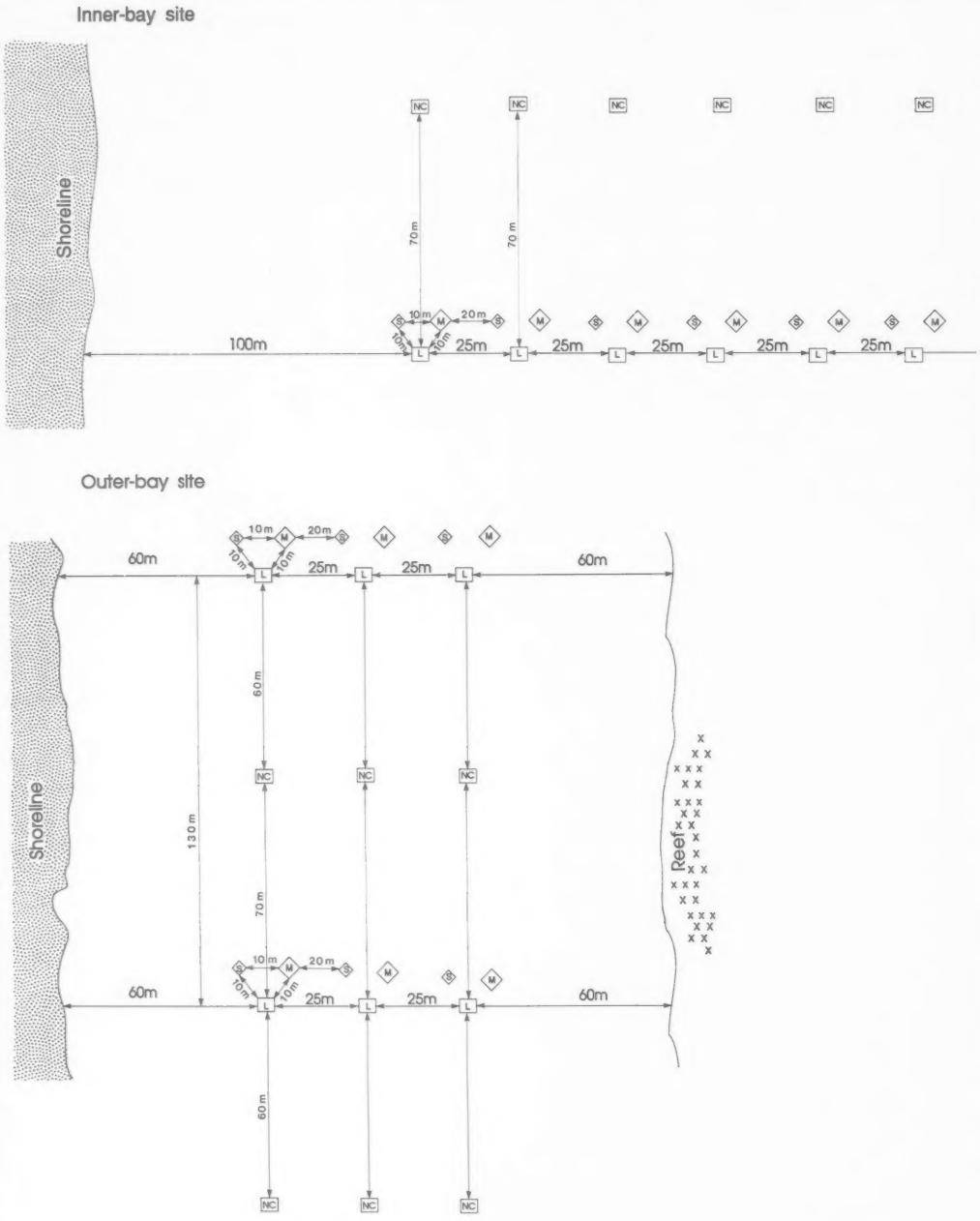


Figure 3

Schematic of casita layout at the (upper) inner-bay and (lower) outer-bay sites for the January 1989 experiment. S = small casita, M = medium casita, L = large casita, and NC = no-casita station.

acrylate cement ensured that a piece of carapace remained on the line as evidence of predator-induced mortality. An empty cable tie without a piece of carapace attached to it was scored as an escape. Each cable-tie was connected with 30 lb test monofilament line either to another cable-tie and attached to a shelter, or attached to a square wire-metal frame that was positioned outside of the triangular casita station (Fig. 3) on the seagrass bed with lead weights. The wire-metal frame had the same length-width dimensions as the large casita but did not provide shelter. The metal frame was chosen over stainless-steel stakes because stakes could not penetrate the underlying carbonate platform at the inner-bay site. The metal frames were visually inconspicuous because they were covered by a thin layer of sediment. Tether lengths of 0.7 m provided a foraging area of about 1.5 m^2 and prevented tangling between adjacent lobsters. Although tethering does not necessarily measure absolute rates of predation, it does measure relative rates of predation (Heck and Thoman 1981), which can serve to compare mortality rates as a function of different experimental treatments.

We used a stationary visual census technique (Bohnsack and Bannerot 1986) to quantify the community structure of potential predators associated with casita and no-casita stations during the experimental period (January and August 1989). Visual censuses were performed between 10:00 and 14:00 hours with three replicate samples taken during the experimental period. By performing the visual censuses during midday, we maximized the visibility available for species identification. Nighttime observations were not performed because our previous study (Eggleston et al. 1990) indicated that the predator guild normally associated with the casitas dispersed widely over the seagrass bed at night. However, predator movements were observed during one dawn and dusk crepuscular period.

We examined the daytime foraging ranges of casita-associated predators by swimming along a transect perpendicular to each casita. When potential predators were observed, a float was set to mark the location, whereupon a scuba diver then followed the predators to assure that they were associated with the casita. Our initial observations indicated that piscine predators associated with casitas seldom moved more than 30–40 m away from a casita.

Experimental design

Before initiating the tethering experiments in 1989, we deployed casitas at the inner-bay and outer-bay sites during 1988. During July 1988 at the inner-bay site, we positioned a row of six large casitas 25 m apart from one another (Fig. 3). Each large casita had one medium and one small casita placed 10 m away, yielding six stations with one small, medium, and large casita arranged in a triangle (Fig. 3). At the outer-bay site during August 1988, we positioned six small, medium and large casitas equidistant between the shore and reef line and arranged these in two rows, each containing three triangular stations (Fig. 3b). See Eggleston et al. (1990) and Eggleston and Lipcius (1992) for a complete description of the small and medium casitas and their use in other field experiments. Two separate tethering experiments were then performed during January and August 1989.

The first experiment was performed during January 1989. In this study we examined the survival of two sizes of juvenile lobsters with and without access to shelter at both the inner-bay and outer-bay sites. Six metal-frame, no-casita stations were placed 60–70 m away and perpendicular to the casitas in sparse-to-moderate-density *Thalassia* at both sites (Fig. 3). Juvenile lobsters were divided into two size-classes: small, 46–55 mm carapace length (CL) as measured dorsally from the base of the supraorbital spines to the posterior border of the cephalothorax; and large, 56–65 mm CL. Lobsters were tethered for 7 days. Each casita and no-casita station at both sites had six tethered lobsters from either of two size-classes for a total of 144 tethered lobsters (2 sites × 6 lobsters × 2 sizes × 2 treatments (casita vs. no-casita) × 3 replicate stations).

Based on our initial observations of predator foraging ranges (see above), we assumed that our choice of 60–70 m for the no-casita station was well beyond the foraging range of diurnally active predators, thereby providing unbiased estimates of lobster survival in the absence of artificial shelters (i.e., mortality estimates were not biased towards finding significantly higher predation rates on lobsters tethered within the foraging range of casita-associated predators). However, our observations during the January 1989 experiment indicated that some predators moved nearly 60 m from the casitas (see Results). Thus, although the 70 m distance from the large casitas was probably beyond the foraging range of casita-associated predators, the 60 m distance from the small and medium casitas was probably not.

Before initiating the second tethering experiment, we positioned a row of three large casitas equidistant between the shore and reef line in July 1989 at the outer-bay site (Fig. 4). In August 1989 we examined how lobster survival varied with distance from the casitas. Three metal-frame no-casita stations were placed 15, 30, and 70 m away and perpendicular to the large casitas (Fig. 4). Based on the foraging ranges of predators during the January experiment (see above), we assumed that 70 m was an adequate distance to

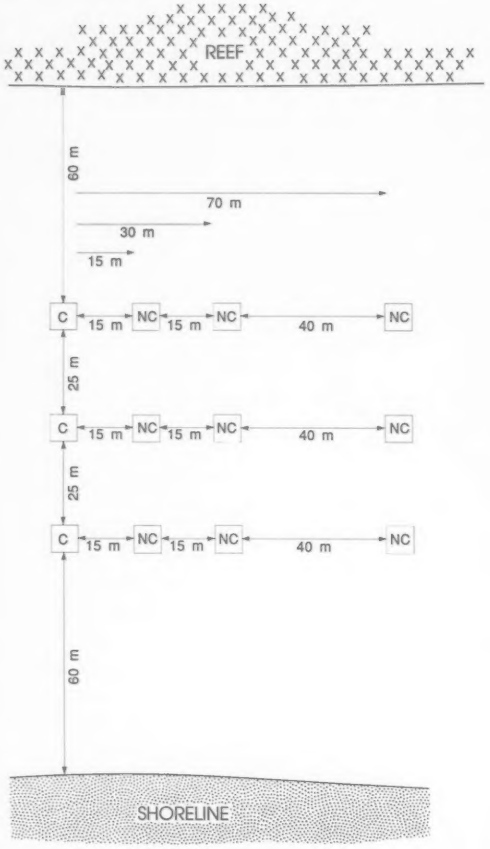


Figure 4

Schematic of casita layout at the outer-bay site for the August 1989 experiment. S = small casita, M = medium casita, L = large casita, and NC = no-casita station.

Table 1

(a) Three-way ANOVA table (model I) describing the effects of site (inner-bay sand-seagrass flat, and outer-bay seagrass bed adjacent to coral reefs), lobster *Panulirus argus* size (small 46–55 mm CL; large 56–65 mm CL) and shelter availability (casita vs. no-casita station 60 m away) on proportional mortality rates (arc-sine square-root transformed) of tethered lobsters during January 1989. $*P<0.05$, $**P<0.01$, ns $P>0.05$.

Source of variation	SS	df	MS	F
Site	0.002	1	0.002	0.402 ns
Lobster size	0.040	1	0.040	7.174**
Shelter availability	0.001	1	0.001	0.006 ns
Site × lobster size	0.001	1	0.001	0.112 ns
Site × shelter availability	0.001	1	0.001	0.235 ns
Lobster size × shelter availability	0.023	1	0.023	4.179*
Site × lobster size × shelter availability	0.001	1	0.001	0.187 ns
Error	0.089	16	0.006	

(b) Ryan's Q tests of mean proportional mortality rates (arc-sine square-root transformed) of tethered lobsters for the interaction effect of lobster size × shelter availability. Treatment levels not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of proportional mortality.

Interaction

Shelter availability	Lobster size	
Casita	large	small
No Casita	large	small

Lobster size	Shelter availability	
Small	Casita	No Casita
Large	No Casita	Casita

assess predation in an environment uninfluenced by the casitas. This assumption held true for the diurnal predator guild during August 1989 (see Results). Only juvenile lobsters approximating the small size-class ($\bar{x}$ 53.2 mm CL, range 45.2–59.0 mm CL, N 72, SD 4.1) were tethered for 7 days. We chose only small lobsters in the second experiment because logistical considerations limited us to one size-class, and we wanted to verify that survival of small lobsters was enhanced when residing beneath casitas (See Results for first experiment below). Each casita and no-casita (i.e., metal frame) station contained 6 tethered lobsters for a total of 72 tethered lobsters (6 lobsters × 4 distances (0, 15, 30, and 70 m) × 3 replicate stations).

Lobsters were checked and predation losses scored every 1–2 days during experiments. Fewer than 4% of tethered lobsters escaped, and these were not used in subsequent statistical analyses. Lobsters that were eaten or missing were not replaced. Cumulative losses were converted to proportional mortality/day/casita (or station). Proportions were analyzed as a function of shelter availability (casita vs. no casita), distance from the casita (0, 15, 30, and 70 m), lobster size (small vs. large), and site (inner-bay vs. outer-bay) with two- and three-way, fixed-factor analyses of variance (ANOVA) models (after procedures in Underwood 1981). Proportional mortality was arc-sine square-root transformed to meet assumptions of normality and homogeneity of variance (Underwood 1981). In all cases, the variances were homogeneous as determined by Cochran's C-test. Differences among means were revealed by use of

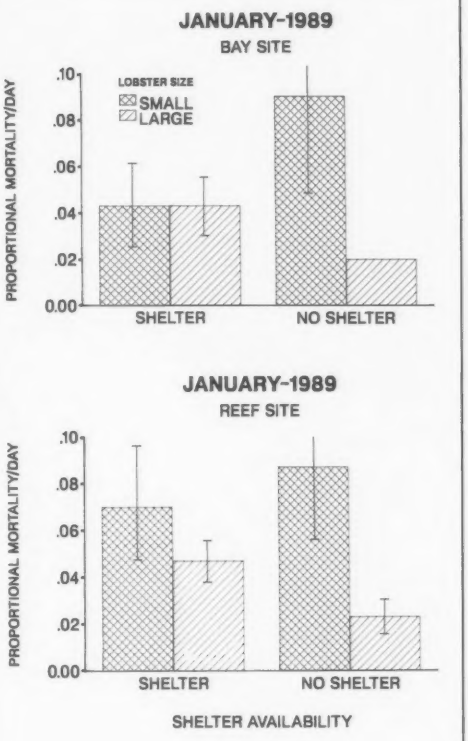


Figure 5

Results of field tethering of *Panulirus argus* at the inner-bay and outer-bay sites during January 1989, describing mortality as a function of lobster size (small 46–55 mm CL; large 56–65 mm CL) and shelter availability (casita vs. no casita). Values are mean proportional mortality · casita^{-1} · d^{-1} resulting from a total of 18 lobsters tested. Vertical bars are 1 SE.

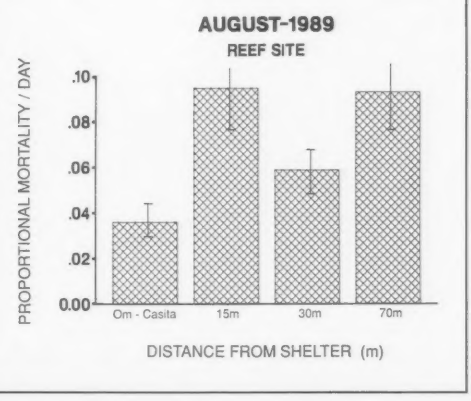


Figure 6

Results of field tethering of *Panulirus argus* at the outer-bay site during August 1989, describing mortality of small juvenile lobsters (46–55 mm CL) as a function of distance from the casita (i.e., 0, 15, 30, and 70 m away from the casita). Values are mean proportional mortality · casita^{-1} · d^{-1} resulting from a total of 18 lobsters tested. Vertical bars are 1 SE.

Ryan's Q multiple comparison test (Einot and Gabriel 1975) as recommended by Day and Quinn (1989).

Results

Tethering experiments

During January 1989, mortality of juvenile lobsters varied significantly as a function of lobster size but not according to site or shelter availability (i.e., tethered to casitas or 60–70 m away in seagrass) (Table 1a, Fig. 5). However, the interaction effect of lobster size by shelter availability was significant; this interaction effect was due to the significantly higher mortality of small vs. large lobsters tethered in seagrass, and by the significantly higher mortality of large lobsters in casitas compared with those tethered in seagrass (Table 1b).

At the outer-bay site in August 1989, mortality rates of small juvenile lobsters varied significantly according to distance from the casita (i.e., 0, 15, 30, and 70 m away from the casita) (Fig. 6; one-way ANOVA; F 5.89, df 3, $P<0.02$). Lobsters suffered significantly higher mortality rates when tethered 15 and 70 m away from casitas than when tethered to casitas or 30 m away from casitas (Fig. 6; Q Ryan's test, experiment-wise error rate 0.05).

Predator observations

The visual census of potential lobster predators at the inner-bay site during January 1989 indicated two predatory crab species (stone crab *Menippe mercenaria*, and a portunid *Portunus spinimanus*) and two piscine predators (gray snapper *Lutjanus griseus*, and schoolmaster snapper *L. apodus*) associated with the casitas (Table 2). No potential predators were observed in the vicinity of the no-casita stations. Mixed schools of gray snapper and schoolmaster snapper were typically found within 10 m of large casitas. Schools associated with small and medium casitas were usually located within 5 m of the casitas. Observed movements of snappers were seldom more than 15–20 m from the shelters. Similarly, two snapper species predominated at the outer-bay site during January 1989: mutton snapper *L. analis* and yellowtail snapper *Ocyurus chrysurus* (Table 2). Casitas at the outer-bay site also attracted octopus (*Octopus* spp.), green moray eel *Gymnothorax funebris*, the stone crab

Table 2

Summary of results from visual census of potential lobster *Panulirus argus* predators associated with 18 casitas of three sizes (small, medium, large) at two sites (inner-bay, outer-bay) during 10–16 January 1989 at Bahia de la Ascension, Mexico. Results below are pooled from censusing 18 casitas on three different sampling dates. Fish size is fork length (cm) and crab size is carapace width (cm).

Species	Total abundance	Mean individuals/ sample/casita	Frequency/ casita size (N 18)	Percent frequency	Size (cm)		
					Mean	Min.	Max.
Inner-bay site							
Large Casita							
Lutjanus griseus (gray snapper)	213	11.8	18	100.0	23.4	9	37
Lutjanus apodus (schoolmaster snapper)	27	1.50	6	33.3	10.0	8	11
Menippe mercenaria (stone crab)	3	0.17	3	16.7	11.0	11	11
Medium Casita							
Lutjanus griseus	12	0.66	12	66.7	7.5	6	10
Menippe mercenaria	2	0.13	2	11.1	7.0	4	10
Portunis spinimanus (portunid crab)	2	0.11	2	11.1	8.0	8	8
Small Casita							
Lutjanus griseus	30	1.67	12	66.7	7.5	6	10
Lutjanus apodus	2	0.11	1	5.6	9.0	9	9
Menippe mercenaria	1	0.06	1	5.6	4.0	—	—
Portunis spinimanus	4	0.22	2	0.1	8.5	7	12
Outer-bay site							
Large Casita							
Lutjanus analis (mutton snapper)	15	0.83	6	33.3	25.3	20	40
Ocyurus chrysurus (yellowtail snapper)	24	1.30	6	33.3	22.0	19	25
Menippe mercenaria	3	0.17	3	16.7	10.0	10	10
Octopus	3	0.16	3	16.7	—	—	—
Medium Casita							
Lutjanus analis	4	0.22	4	22.2	12.8	10	15
Portunis spinimanus	2	0.11	2	11.1	9.5	6	13
Small Casita							
Lutjanus analis	3	0.16	2	11.1	8.0	8	8
Gymnothorax funebris (green moray eel)	3	0.16	3	16.7	50.0	50	50
Portunis spinimanus	3	0.16	3	16.7	7.5	6	11

M. mercenaria, and the portunid crab *P. spinimanus* (Table 2). As above, no potential predators were observed in the vicinity of the no-casita stations, and mixed schools of snapper seldom strayed more than 15–20 m from casitas. However, several large snapper of both species (*L. griseus* at the inner-bay site and *L. analis* at the outer-bay site) were observed ~60 m from the casitas. We also witnessed a stone crab feeding on a lobster tethered beneath a casita, and on two separate occasions observed octopus feeding on tethered lobsters beneath a casita.

During January 1989 at the inner-bay site, there was a significant positive correlation between mean lobster proportional mortality per day at a particular casita station and the mean number of potential predators occupying the same casita station (r 0.92, n 6, $P<0.01$; Fig. 7). Conversely, there was no significant correlation between lobster proportional mortality and numbers of predators inhabiting casitas at the outer-bay site (r 0.11, n 6, NS), nor between proportional mortality and the sizes of piscine predators (mm total length; TL) at both sites (inner-bay: r 0.64, n 6, NS; outer-bay: r 0.59, n 6, NS).

Predator observations at the outer-bay site in August demonstrated a more diverse predator guild than that observed during January (compare Tables 2 and 3). Although mutton snapper and yellowtail snapper were abundant at large casitas, they were joined by larger predators, including Nassau grouper *Epinephelus striatus* and a great barracuda *Sphyraena barracuda*. One barracuda was identified by particular scars near the mouth and a broken tooth. This barracuda roamed the entire experimental area. We also observed one Nassau grouper that moved between the 70 m no-casita stations and the reef (see Fig. 4 for geography). Another slightly smaller grouper moved back and forth between the casitas, the 15 m no-casita stations, and the reef.

Table 3

Summary of results from visual census of potential lobster *Panulirus argus* predators associated with three large casitas at the outer-bay site during 3–10 August 1989 at Bahia de la Ascension, Mexico. Results below are pooled from censusing three casitas on three different sampling dates. Fish size is fork length (cm).

Species	Total abundance	Mean individuals/ sample/casita	Frequency/ casita size (N 18)	Percent frequency	Size (cm)		
					Mean	Min.	Max.
Lutjanus analis (mutton snapper)	12	1.33	9	100.0	20.3	15	30
Ocyurus chrysurus (yellowtail snapper)	15	1.67	9	100.0	22.0	19	25
Sphyraena barracuda (great barracuda)	2	0.22	2	22.2	100.0	100	100
Epinephelus striatus (Nassau grouper)	2	0.22	2	22.2	45.0	40	50
Dasyatis americana (southern stingray)	1	0.11	1	11.1	60.0*	—	—

*Measured from wingtip to wingtip (cm).

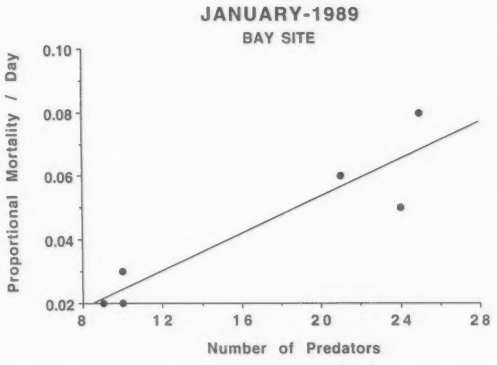


Figure 7

Mean proportional mortality of juvenile lobsters *Panulirus argus* · large casita^{-1} · d^{-1} compared against the mean number of potential predators · casita station^{-1} · d^{-1} at the inner-bay site during January 1989 ($y = -0.0051 + 0.0029x$; r^2 0.85, n 6, $P<0.009$).

Discussion

The impact of artificial shelters upon juvenile spiny lobster survival varied both by lobster size and the distance of unprotected lobsters from shelter. During our January 1989 experiment, which emphasized the effects of lobster size and shelter availability, large lobsters (56–65 mm CL) survived better than small lobsters (46–55 mm CL) in sparse-to-moderate-density seagrass (*Thalassia*) 60 m from casitas. Conversely, small lobsters survived better than large lobsters when tethered beneath casitas. During our August 1989 experiment, small lobsters survived better at casitas or 30 m away from casitas than 15 m or 70 m away. We interpret these patterns in terms of the relative importance of shelter availability and body size upon lobster survival, and then speculate on the influence of artificial-shelter-associated predators and seagrass density relative to these patterns in lobster survival.

We reemphasize that predation estimates based on tethering are likely biased by the technique and may not reflect natural predation rates. For example, lobster dens which are normally abandoned at night may become "traps" for tethered lobsters because they cannot effectively flee and conspecifics are not available to help detect and repel predators. However, predation rates on early juvenile *Panulirus argus* tethered in open sand, seagrass, and algal habitats in Florida Bay were similar both day and night (Herrnkind and Butler 1986, Smith and Herrnkind 1992). Moreover, most casita-associated predators are widely dispersed among the seagrass flats at night in Bahia de la Ascension, Mexico (Eggleston et al. 1990). Thus, we feel that the tethering technique is not only useful for comparing relative rates of predation between different size-classes of juvenile spiny lobster, but also for comparing predation rates between representative benthic habitats (e.g., crevices, algal clumps, seagrass).

Results from our January 1989 experiment support the hypothesis that large juvenile lobsters (56–65 mm CL) attain a relative-size refuge from predation compared with small juvenile lobsters (45–55 mm CL), and that the relative importance of this size refuge varies according to shelter availability. Increased predation

on small juvenile lobsters tethered in seagrass suggests that sparse-to-moderate-density *Thalassia* does not provide adequate protection from predators, and that the addition of shelter greatly enhances survival for these smaller juvenile lobsters. Thus, the use of artificial lobster shelters in sparse-to-moderate-density *Thalassia* beds may effectively reduce predation-induced mortality rates of small juvenile lobsters and thereby enhance production of this size-class. However, given the general relationship of increasing survival with habitat complexity for many decapod crustaceans (Heck and Thoman 1981, Wilson et al. 1987, Heck and Crowder 1991 and references therein), the relative importance of shelter availability upon survival of small juvenile lobsters may be reduced in habitats with dense *Thalassia*. Thus, further studies are required to understand the relationship between shelter availability and increasing habitat complexity upon survival of small juvenile lobsters.

The reduced survival of large juvenile lobsters near casitas compared with seagrass 60–70 m away during the January 1989 experiment is consistent with our previous results for this lobster size-class. For example, survival of small lobsters (46–55 mm CL) in large casitas was significantly higher than survival of large lobsters (56–65 mm CL) (Eggleston et al. 1990). Moreover, large lobsters survived better in medium than in large casitas (Eggleston et al. 1990). Eggleston et al. (1990) suggested that medium casitas excluded predators that were able to prey on large lobsters, and postulated that larger predators associated with large casitas may selectively prey upon larger lobsters, due to better visual perception with increasing predator and prey size (Kao et al. 1985, Ryer 1988). The significant positive correlation between the numbers of predators (primarily gray snapper *L. griseus*) occupying specific casita stations and predation rates at these same stations suggests that gray snapper may be the principle predator of juvenile lobsters inhabiting casitas at the inner-bay nursery site. Gray snapper (15 cm TL) have successfully attacked small early-juvenile lobsters tethered in Florida Bay (Herrnkind and Butler 1986).

The combined results from this study and previous work in Bahia de la Ascension, Mexico (Eggleston et al. 1990), suggest that juvenile lobsters would survive better by leaving large shelters to take up residence in smaller shelters or nearby seagrass habitats when they reach a body size of ~56–65 mm CL. This idea of enhancing survival through size-specific emigration from large shelters was partially supported during our recent observations of habitat-specific and size-specific patterns of shelter use by juvenile *P. argus* in Bahia de la Ascension, Mexico. Our recent field observations (Eggleston and Lipcius 1992) indicated that shelter-seeking behavior of *P. argus* is highly flexible to local social conditions (i.e., presence of conspecifics) and shelter scaling. For example, in a habitat containing very few conspecifics (e.g., outer-bay site), large juvenile lobsters chose smaller, safer medium casitas over large casitas as predicted by our tethering results (this study; Eggleston et al. 1990). However, in a habitat containing large numbers of conspecifics (e.g., inner-bay site), large juvenile lobsters occupied large casitas with large conspecifics (Eggleston and Lipcius 1992). The tethering technique in this study did not address the potential benefits of gregarious residency to lobster survival. Gregarious occupancy by more than the six tethered lobsters appeared to be inhibited because of the tethering technique, i.e., lobsters did not colonize casitas containing tethered individuals (pers. observ.). Since gregarious sheltering has been implicated as a mechanism for reducing predator-induced mortality (Berrill 1975, Herrnkind et al. 1975, Eggleston and Lipcius 1992), final conclusions regarding the impact of casitas upon predation-induced mortality rates of large juvenile lobsters must not only consider the size-specific relationship between shelter-associated predators and lobsters, but also the potential benefits of gregarious sheltering.

Results from our August 1989 experiment support the hypothesis that the impact of artificial shelters upon predation-induced mortality of juvenile lobsters varies according to the distance of unprotected lobsters from these shelters. During the August experiment at the outer-bay site, small lobsters survived equally well whether they were tethered beneath casitas or 30 m away. These tethering results, combined with observations on predator movements, suggest that 30 m is beyond the daytime foraging range of most casita-associated predators. However, the lack of a significant correlation between the numbers of potential predators at a specific casita station and predation rates on lobsters at these same stations at the outer-bay site during the January 1989 experiment suggests that transient predators such as jacks (*Caranx* spp.), groupers (*Epinephelus* spp.), sharks (*Ginglymostoma cirratum* and *Sphyrna* spp.), and stingrays (*Dasyatis* spp.) may be moving from the nearby barrier reef (see Figs. 3 and 4 for geography) and preying on tethered lobsters. Gut contents of stingrays (*Dasyatis* spp.) and bonnethead sharks *Sphyrna tiburo*, captured at night in nearshore Florida Bay waters, contained a high proportion of early-juvenile spiny lobsters (Smith and Herrnkind 1992). Nurse sharks *Ginglymostoma cirratum* are also known predators of juvenile *P. argus* (Cruz and Brito 1986). Thus, our observations on the daytime abundance and movements of casita-associated predators (i.e., primarily mutton and yellowtail snapper, *Lutjanus analis* and *O. chrysurus*) at the outer-

bay site may not reflect potential predation intensity as previously suggested for the inner-bay site.

Predation risk on artifical reefs usually decreases with distance from a natural, larger reef. For example, mortality of tethered juvenile grunts (family Pomadasyidae) in St. Croix, U.S. Virgin Islands, was 40% higher at the reef edge than 20 m away (Shulman 1985). Our results are somewhat consistent with those of Shulman (1985) in that predation of lobsters decreased from 15 to 30 m from the casitas. However, increased predation rates from 0 to 15 m and from 30 to 70 m indicate that predation risk does not simply decrease linearly with increasing distance from the artificial reef (casita). We hypothesize that the predator guild originating from the nearby barrier reef at the outer-bay site (see Figs. 3 and 4 for geography) forages within the adjacent seagrass habitat and is attracted to the casitas, thereby leaving a relative "gap" in predator abundance between 15 and 60 m from the casitas. Thus, predator encounter rates with lobsters tethered only 15 m from casitas were probably high relative to lobsters tethered 30 m away. The patterns of survival of small *P. argus* within close proximity to casitas (i.e., 15 m) in this study are consistent with our previous work in seagrass habitats of Bahia de la Ascension, Mexico. For example, survival of small lobsters (46–55 mm CL) was significantly higher at medium and large casitas than in seagrass 15 m away (Eggleston et al. 1990). Predation rates also increased from 30 to 70 m, and predators not associated with the casitas, such as Nassau grouper *E. striatus*, were observed moving from nearby natural reefs to the 70 m no-casita stations rather than from the casitas.

Resident piscivores set the upper limit of the number and sizes of prey species that can occupy a given reef (Hixon and Beets 1989, Eggleston et al. 1990). For example, Hixon and Beets (1989) found an inverse relationship between the number of piscivorous fishes on a reef and the maximum number of co-occurring potential prey fishes. The results from our study indicate that large casitas are more effective at reducing mortality on small juvenile lobsters than seagrass habitats, even though seagrass and algal beds provide some refuge for juvenile spiny lobsters (Herrnkind and Butler 1986; R.N. Lipcius et al., unpubl. data). Hence, for small lobsters, our results from both the January and August experiments strongly suggest that artificial lobster shelters such as casitas increase lobster production by enhancing survival in nursery areas. However, our results for the outer-bay site during January indicated that survival of large juvenile lobsters was significantly lower when tethered beneath large casitas compared with nearby seagrass habitats. These results are consistent with the notion of building artificial lobster shelters that are scaled according to body size to enhance survival of larger juveniles in nursery habitats, particularly in areas where large conspecifics are removed from large casitas by the fishery (Eggleston et al. 1990, Eggleston and Lipcius 1992). However, further research on the impact of casitas upon lobster survival, growth rates, local and regional population structure, and benthic community structure will be required to assess the efficacy of this technology as a fisheries enhancement tool.

Acknowledgments

We thank L. Coba-Cetina, T. Camarena-Luhrs, and E. Sosa-Cordero with the Centro de Investigaciones de Quintana Roo, and J. Cohen, J. Eggleston, K. Kennedy, and numerous Earthwatch volunteers for their able field assistance. Special thanks to Armando Lopez and Sonja Lillvick for the fine accommodations and logistical support, and R. Wicklund and G. Wenz of the Caribbean Marine Research Center for their administrative guidance. We thank J. Bohnsack, L. Jones, M. Luckenbach, J. van Montfrans, and two anonymous referees for critical comments. This work was funded by Sigma-Xi, Earthwatch–The Center for Field Research, the National Undersea Research Program of the National Oceanic and Atmospheric Administration, the Caribbean Marine Research Center, the Commonwealth of Virginia, L.L. Glucksman, and the National Science Foundation (INT-8617945 to D.M. and R.L. and OCE 87-00414 to R.L. and A. Hines).

Citations

Berrill, M.
1975 Gregarious behavior of juveniles of the spiny lobster, *Panulirus argus* (Crustacea: Decapoda). Bull. Mar. Sci. 25: 515–522.

Bohnsack, J.A.
1989 Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bull. Mar. Sci. 44:631–645.

Bohnsack, J.A., and S.P. Bannerot
1986 A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Tech. Rep. NMFS 41, 15 p.

Bohnsack, J.A., and D.L. Sutherland
1985 Artificial reef research: A review with recommendations for future priorities. Bull. Mar. Sci. 37:11–39.

Cobb, J.S.
1981 Behaviour of the Western Australian spiny lobster, *Panulirus cygnus* George, in the field and laboratory. Aust. J. Mar. Freshwater Res. 31:399–409.

Cruz, R., and R. Brito
1986 Ecologia de la langosta (*Panulirus argus*) al SE de Isla de la Juventud. I. Colonizacion de arrecifes artificiales. Rev. Invest. Mar. 7:3–17.

Day, R.W., and G.P. Quinn
1989 Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59:433–463.

Eggleston, D.B., and R.N. Lipcius
1992 Shelter selection by spiny lobster under variable predation risk, social conditions and shelter size. Ecology 73: 992–1011.

Eggleston, D.B., R.N. Lipcius, D.L. Miller, and L. Coba-Cetina
1990 Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. Mar. Ecol. Prog. Ser. 62: 70–88.

Einot, I., and K.R. Gabriel
1975 A study of the powers of several methods of multiple comparisons. J. Am. Stat. Assoc. 70:574–583.

Grove, R.S., and C.J. Sonu
1985 Fishing reef planning in Japan. *In* D'Itri, F. (ed.), Artificial reefs: Marine and freshwater applications, p. 187–251. Lewis Publ., Chelsea, MI.

Hartnoll, R.G.
1982 Growth. *In* Abele, L.G. (ed.) The biology of crustacea, vol. 2, p. 111–196. Academic Press, NY.

Heck, K.L. Jr., and L.B. Crowder
1991 Habitat structure and predator-prey interactions in vegetated aquatic systems. *In* Bell, S.S., E.D. McCoy, and H.R. Mushinsky (eds.), Habitat structure: The physical arrangement of objects in space, p. 281–299. Chapman & Hall, NY.

Heck, K.L. Jr., and T.A. Thoman
1981 Experiments on predator-prey interactions in vegetated aquatic habitats. J. Exp. Mar. Biol. Ecol. 53:125–134.

Herrnkind, W.F., and M.J. Butler
1986 Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. Mar. Ecol. Prog. Ser. 34:23–30.

Herrnkind, W.F., J. Vanderwalker, and L. Barr
1975 Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S. Virgin Islands: Habitation and pattern of movements. Sci. Bull., Nat. Hist. Mus., Los Angel. Cty. 20:31–34.

Hixon, M.A., and J.P. Beets
1989 Shelter characteristics and Caribbean fish assemblages: Experiments with artificial reefs. Bull. Mar. Sci. 44:666–680.

Howard, R.K.
1988 Fish predators of the western rock lobster (*Panulirus cygnus* George) in a nearshore nursery habitat. Aust. J. Mar. Freshwater Res. 39:307–316.

Kao, T., T.K. Wetterer, and N.G. Hairston Jr.
1985 Fish size, visual resolution and prey selectivity. Ecology 66:1729–1735.

Lozano-Alvarez, E., P. Briones-Fourzan, and B.F. Phillips
1991 Fishery characteristics, growth, and movements of the spiny lobster *Panulirus argus* in Bahia de la Ascension, Mexico. Fish. Bull., U.S. 89:79–89.

Miller, D.L.
1989 Technology, territoriality and ecology: The evolution of Mexico's Caribbean spiny lobster fishery. *In* Barkes, F. (ed.), Common property resources: Ecology and community-based sustainable development, p. 185–198. Valhaven Press, London.

Mottet, M.G.
1985 Enhancement of the marine environment for fisheries and aquaculture in Japan. *In* D'Itri, F. (ed.), Artificial reefs: Marine and freshwater applications, p. 13–112. Lewis Publ., Chelsea, MI.

Munro, T.
1974 The biology, ecology, and bionomics of Caribbean reef fishes. Part VI. Crustaceans (spiny lobsters and crabs). Univ. West Indies Zool. Dep., Res. Rep. 3:1–57.

Reaka, M.L.
1987 Adult-juvenile interactions in benthic reef crustaceans. Bull. Mar. Sci. 41:108–134.

Ryer, C.H.
1988 Pipefish foraging: effects of fish size, prey size and altered habitat complexity. J. Exp. Mar. Biol. Ecol. 48:37–45.

Scully, E.P.
1983 The behavioral ecology of competition and resource utilization among hermit crabs. *In* Rebach, S., and D.W. Dunham (eds.), Studies in adaptation: The behavior of higher Crustacea, p. 23–56. John Wiley, NY.

Shulman, M.J.
1985 Recruitment and coral reef fishes: Effects of distribution of predators and shelter. Ecology 66:1056–1066.

Smith, K.N., and W.F. Herrnkind
1992 Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): Influence of size and shelter. J. Exp. Mar. Biol. Ecol. 157:3–18.

Underwood, A.
1981 Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Annu. Rev. 19: 513–605.

U.S. Agency for International Development
1987 Caribbean marine resources: Oppurtunities for economic development and management. U.S. Agy. Int. Develop., Wash. DC, 53 p.

Vermeij, G.
1987 Evolution and escalation: An ecological history of life. Princeton Univ. Press, Princeton, 527 p.

Wilson, K.A., K.L. Heck Jr., and K.W. Able
1987 Juvenile blue crab, *Callinectes sapidus*, survival: An evaluation of eelgrass, *Zostera marina*, as refuge. Fish. Bull., U.S. 85:53–58.

Zimmer-Faust, R.K., and E. Spanier
1987 Gregariousness and sociality in spiny lobsters: Implications for den habitation. J. Exp. Mar. Biol. Ecol. 105:57–71.

Stock structure of the bluefish *Pomatomus saltatrix* along the mid-Atlantic coast*

John E. Graves
Jan R. McDowell
Ana M. Beardsley
Daniel R. Scoles

Virginia Institute of Marine Science, School of Marine Science
College of William and Mary, Gloucester Point, Virginia 23062

Abstract.–Restriction-fragment length polymorphism analysis of mitochondrial DNA (mtDNA) was used to investigate the genetic basis of stock structure of the bluefish *Pomatomus saltatrix* along the U.S. mid-Atlantic coast, and to determine the degree of genetic differentiation between mid-Atlantic bluefish and Australian conspecifics. A total of 472 young-of-the-year (YOY) and yearling bluefish collected in New Jersey, Virginia, and North Carolina over a period of 3 years, and 19 YOY bluefish collected in New South Wales, Australia were analyzed with 9 informative restriction endonucleases. Despite considerable mtDNA variation within samples of U.S. mid-Atlantic bluefish, no significant genetic differentiation was detected among spring-spawned and summer-spawned (YOY) bluefish, YOY and yearling bluefish from different geographic locations along the mid-Atlantic coast, or yearling bluefish collected at the same location in different years. Mid-Atlantic bluefish differed from their Australian conspecifics by three or more restriction site differences, or a mean nucleotide sequence divergence of 1.96%. In addition, Australian bluefish demonstrated greatly reduced levels of mtDNA variation relative to the mid-Atlantic samples. The results of this study suggest that bluefish along the mid-Atlantic coast comprise a single genetic stock and that significant differentiation occurs among geographically disjunct populations of this widely distributed marine fish.

Manuscript accepted 29 July 1992.
Fishery Bulletin, U.S. 90:703–710 (1992).

The bluefish *Pomatomus saltatrix* is broadly distributed in temperate and warm-temperate coastal waters of the world's oceans (Briggs 1960), although it is absent from the eastern Pacific (Smith 1949). In the United States, bluefish occur along the Atlantic and Gulf coasts, supporting large recreational and commercial fisheries.

The movements and biology of the bluefish, like many fishes along the Atlantic coast, are closely tied to large seasonal fluctuations in water temperature (reviewed in Wilk 1977). Spawning appears to be concentrated in two spatially and temporally distinct events: a spring spawn at the inside edge of the Gulf Stream in the south Atlantic bight, and a summer spawn in the shelf waters of the mid-Atlantic bight (Kendall and Walford 1979). However, the presence of eggs and larvae indicates that some spawning occurs throughout the year, especially in the southern portion of the south Atlantic bight (Kendall and Walford 1979, Collins and Stender 1988). Presumably, eggs and larvae are transported by cross-shelf currents to estuaries along the Atlantic coast which serve as nursery grounds for the young bluefish.

The discrete temporal nature of the two spawning events is evidenced by a bimodal size distribution of juvenile bluefish within the estuaries during the middle and late summer (Nyman and Conover 1988, McBride 1989), a difference that is still evident in yearling fish and may persist until fish reach 4 years of age (Lassiter 1962). The extent to which each of the major spawning events contributes juveniles to specific areas appears to vary annually (Chiarella and Conover 1990).

A general mixing of bluefish from different coastal areas may occur at the end of the first summer. Tagging studies indicate that as water temperatures cool, young bluefish move out of the estuaries in a southerly direction and probably overwinter in the south Atlantic bight (Lund and Maltezos 1970, Wilk 1977), while adults move further offshore (Wilk 1977). As temperatures along the mid-Atlantic coast warm in the spring, there is a general movement of bluefish up the Atlantic coast, with larger bluefish making more extensive migrations into northern waters (Wilk 1977).

Although the seasonal movements of bluefish may be conducive to a mixing of fish from different coastal areas, mark and recapture studies suggest that a large fraction of bluefish are recaptured in the same general area in which they were tagged (Lund and Maltezos 1970, Wilk 1977). The degree to which this fidelity affects stock structure is not known.

*Contribution 1750 of the Virginia Institute of Marine Science.

Table 1

Sample size, date, location, and age of bluefish *Pomatomus saltatrix* collected and analyzed in this study. YRL = yearling; YOY = young-of-the-year.

Sample	*n*	Date	Location	Age
VA88	100	7/88	York River VA	YRL
VA89	102	7/89	York River VA	YRL
VA90	39	7/90	York River VA	YRL
NC88	83	7/88	Hatteras NC	YRL
NC89	57	7/89	Hatteras NC	YRL
NC90	40	7/90	Hatteras NC	YOY
NJ90-Sp	26	8/90	southern NJ	YOY
NJ90-Su	25	8/90	southern NJ	YOY
AU91	19	2/91	Port Stephens, N.S.W., Australia	YOY

The genetic basis of population structure of the bluefish is poorly understood. Based on studies of morphological and scale characteristics, Wilk (1977) suggested that two populations exist along the mid-Atlantic coast. These populations correspond to the fish which spawn off North Carolina in the spring, and those that spawn in the northern mid-Atlantic during the summer. Lund and Maltezos (1970) also concluded on the basis of mark and recapture analysis that several populations are present along the mid-Atlantic coast. Chiarella and Conover (1990) used scales from summer-spawning fish in the New York Bight to back-calculate length at age-1 and found that most summer-spawning fish had lengths corresponding to a spring birthdate, a result not consistent with spring- and summer-spawning stocks. They concluded that the morphological and life-history differences found between spring- and summer-spawned bluefish are probably ecophenotypic in nature, and suggested that a direct genetic analysis of stock structure was warranted.

In this paper, we present the results of a restriction-fragment length polymorphism (RFLP) analysis of bluefish mitochondrial DNA (mtDNA) among bluefish collected along the mid-Atlantic coast over a period of 3 years. We employed RFLP analysis of mtDNA to evaluate genetic differentiation between spring- and summer-spawned bluefish collected at a single location at the same time, among similarly-sized bluefish collected at the same location over several years, and among bluefish collected during the same year from the north and south mid-Atlantic coast, as well as from a disjunct population in Australia.

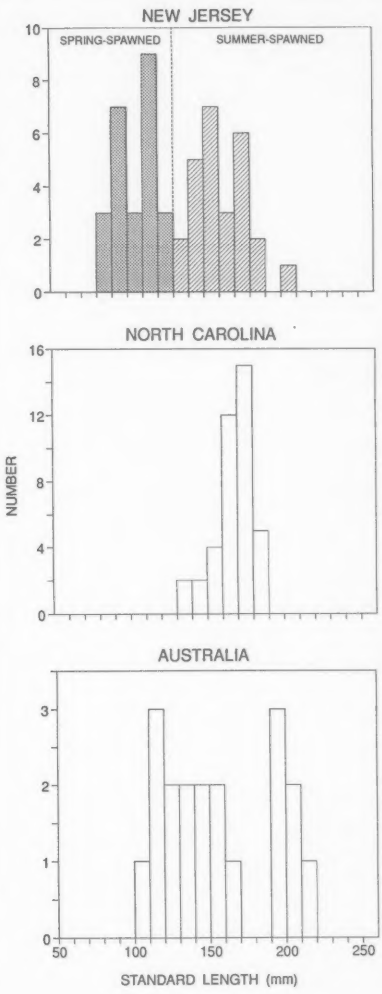


Figure 1

Frequency distribution of standard lengths among YOY bluefish *Pomatomus saltatrix* collected in New Jersey, North Carolina, and Port Stephens, N.S.W., Australia. The New Jersey fish were separated into spring- and summer-spawned groups based upon their standard length on the date of capture relative to a standard length of 125 mm (Nyman and Conover 1988, McBride 1989).

Materials and methods

Experimental design and collections

Bluefish were collected along the mid-Atlantic coast during 1988–90, and in Australia during 1991 (Table 1). To test the hypothesis that spring- and summer-spawned bluefish represent genetically distinct stocks, young-of-the-year bluefish were collected by trawl on New Jersey state survey cruises during August 1990 (NJ90-Sp, NJ90-Su, Table 1). Fish were classified as spring- or summer-spawned based on the date of capture using a standard length of 125 mm used as the cut-off between the two groups in August (Nyman and Conover 1988, McBride 1989). The distribution of lengths is presented in Figure 1.

To obtain an estimate of the degree of temporal genetic variation between bluefish year-classes at a single collection location, 1-year-old (yearling) bluefish were purchased from commercial fishermen on the York River, Virginia during July 1988 (VA88), 1989 (VA89), and 1990 (VA90), and in Hatteras, North Carolina during 1988 (NC88) and 1989 (NC89). The distribution of lengths of the Virginia and North Carolina samples is presented in Figure 2.

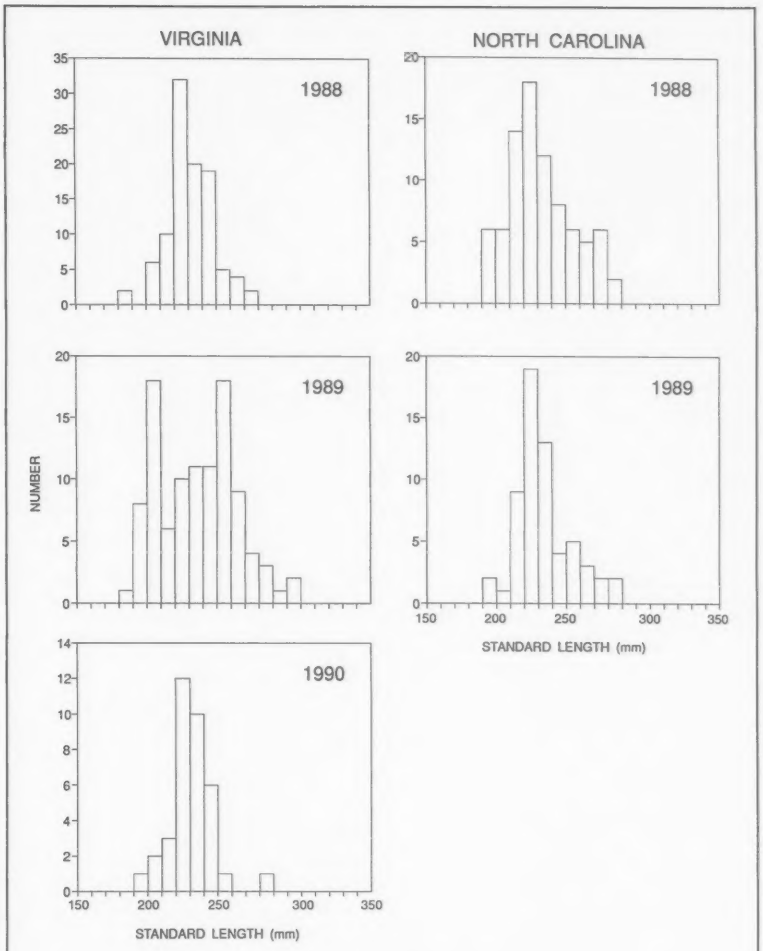


Figure 2

Frequency distribution of standard lengths among yearling bluefish *Pomatomus saltatrix* collected in (left) the York River, VA during summer 1988, 1989, and 1990, and (right) Hatteras, NC during summer 1988 and 1989.

An analysis of geographic population structure of highly vagile fishes, like the bluefish, is problematic. The presence of an adult bluefish in one geographic location is not very meaningful, as the fish could easily travel to another location several hundred kilometers away within a few weeks. If discrete geographic stocks of bluefish exist, such stocks might be expected to separate at the time of spawning. However, collection of adults at this critical time is difficult since bluefish spawn at the edge of the continental shelf during the spring and in the middle of the shelf during the summer (Kendall and Walford 1979). Thus we decided to focus our study on their products, YOY bluefish. Although some mixing probably occurs during cross-shelf transport, the genetic composition of YOY bluefish should reflect the composition of the offshore spawning population.

To determine genetic differentiation among bluefish along the mid-Atlantic coast, samples of YOY individuals were collected during summer 1990 in New Jersey (described above) and purchased from commercial fishermen in Hatteras, North Carolina (NC90). In addition, to obtain an estimate of the degree of mtDNA differentiation between isolated bluefish populations, a sample of 19 YOY bluefish was collected by hook-and-line in Port Stephens, N.S.W., Australia during February 1991 (AU91). The size composition of all YOY collections is presented in Figure 1.

mtDNA analysis

Depending on size and quality of the bluefish, three different procedures were used to analyze bluefish mtDNA. The rapid isolation procedure of Chapman and Powers (1984) was used to obtain mtDNA from samples of lateral red muscle from the yearling bluefish collected in 1988 and 1989. After digestion, restriction fragments were separated electrophoretically on 0.8–1.5% agarose gels run at 2 volts/cm overnight and visualized directly with ethidium bromide staining. For those samples in which there was not sufficient mtDNA

for direct visualization, restriction digestions were endlabeled before electrophoresis with a mixture of all four ^{35}S nucleotide triphosphates using the Klenow fragment (Maniatis et al. 1982). After electrophoresis, gels were treated with a scintillation enhancer, dried, and autoradiographs exposed at −70°C for 5 days.

Mitochondrial DNA was purified from YOY and yearling bluefish collected in 1990 and 1991 following the protocols of Lansman et al. (1981) and ^{35}S-end-labeled restriction fragments were visualized autoradiographically after electrophoresis. Due to the thermal history of many of these specimens, yields of supercoiled mtDNA were low. In those instances, the nuclear band containing both nuclear DNA and relaxed mtDNA was collected and dialyzed as described for mtDNA bands in Lansman et al. (1981), or mtDNA was reisolated following the Chapman and Powers (1984) protocol. For these samples, the Southern transfer and

Table 2

Distribution of mtDNA genotypes among bluefish *Pomatomus saltatrix* samples. Each letter represents the fragment pattern for a particular restriction endonuclease: from left to right, *Ava*I, *Hin*dIII, *Pvu*II, *Dra*I, *Eco*RV, *Sst*I, *Pst*I, *Sst*II, and *Nci*I. A description of all fragment patterns and sizes is available from the authors upon request.

Composite genotype	VA88	VA89	VA90	NC88	NC89	NC90	NJ90-Sp	NJ90-Su	AU91	Total
AAAAAAAAA	44	45	24	50	33	17	20	18	0	250
AAAAAAAAB	0	0	0	1	1	1	0	0	0	3
AAAAAAAAC	1	2	0	1	1	0	0	2	0	7
AAAAAAAAD	6	1	0	0	0	0	0	0	0	7
AAAAAAAAG	0	1	1	0	1	0	0	0	0	3
AAAAAAAAH	0	0	1	0	0	0	0	0	0	1
AAAAABAAA	0	0	1	0	0	0	0	1	0	2
AAAABAAAA	11	11	1	5	3	5	1	1	0	38
AAAABAAAB	0	0	0	0	1	0	0	0	0	1
AAAABAABA	0	1	0	1	0	0	0	1	0	3
AAAACAAAA	6	6	3	2	3	2	2	0	0	24
AAAACAAAC	0	0	0	0	0	1	0	0	0	1
AAAACAABA	0	0	0	0	0	1	0	0	0	1
AAAADAAAA	7	13	3	4	2	4	1	1	0	35
AAABAAAAA	0	0	1	0	1	0	0	0	0	2
AAACAAAAA	1	1	0	1	0	0	0	0	0	3
AAAEEAAAD	0	0	0	0	0	0	0	0	18	18
AAAEFAAAD	0	0	0	0	0	0	0	0	1	1
AABAAAAAA	0	2	0	1	1	0	0	0	0	4
AABABAAAA	3	4	0	2	1	3	1	0	0	14
AABABAAAB	1	0	0	0	0	0	0	0	0	1
AABABAAAC	0	0	0	0	1	0	0	0	0	1
AABABAAAE	0	2	0	2	0	1	0	0	0	5
AACAAAAAA	1	0	0	2	1	0	0	0	0	4
AACACAAAA	2	2	0	0	0	0	0	0	0	4
BAAAAAAAA	6	2	0	4	3	2	0	1	0	18
BAAAAAAAC	0	1	0	0	0	0	0	0	0	1
BAAACAAAA	5	1	0	2	0	0	0	0	0	8
BAAACAAAD	1	0	0	0	0	0	0	0	0	1
BAAACBAAA	0	1	0	0	0	0	0	0	0	1
BAAADAAAA	0	0	0	1	1	0	0	0	0	2
BADAAAAAA	1	0	0	0	0	0	0	0	0	1
BADACAAAA	0	0	0	1	0	0	0	0	0	1
CAAAAAAAA	1	1	0	0	1	0	0	0	0	3
CAAAAAAAC	3	1	1	0	0	2	0	0	0	8
CAAABAAAC	0	1	0	0	0	0	0	0	0	1
DAAAAAAAA	0	2	0	1	1	1	0	0	0	5
DAAACAAAA	0	1	0	0	0	0	0	0	0	1
DACAAAAAA	0	0	0	0	1	0	0	0	0	1
EAAAAAAAF	0	0	0	1	0	0	0	0	0	1
FAAAAAAAA	0	1	0	1	0	0	0	0	0	2
Totals	100	102	36	83	57	40	26	25	19	469

hybridization protocols of Maniatis et al. (1982) were followed after digestion and electrophoresis. Highly purified bluefish mtDNA, nick translated with biotin-7-dATP, was used as a probe for mtDNA fragments. Hybridization filters were visualized after strigency washes using the BRL BlueGene Nonradioadtive Nucleic Acid Detection System.

All mtDNA samples were digested with the following nine restriction endonucleases used according to the manufacturers' instructions: *Ava*I, *Dra*I, *Eco*RV, *Hin*dIII, *Nci*I, *Pst*I, *Pvu*II, *Sst*I, and *Sst*II. The different restriction-fragment patterns produced by each restriction endonuclease were assigned a letter, and a composite mtDNA genotype, consisting of nine letters representing the fragment patterns generated by each of the restriction endonucleases, was constructed for each individual. The nucleon diversity (Nei 1987) was calculated for each sample and for the pooled samples. The nucleotide sequence divergence among mtDNA genotypes was estimated by the site approach of Nei and Li (1979). The mean nucleotide sequence diversity within samples and mean nucleotide sequence divergence between samples were calculated following the method of Nei (1987), with the latter value being corrected for within-group diversity (Nei 1987). The distribution of genotypes was evaluated for homogeneity among collections using the G-test (Sokal and Rohlf 1981); however, as several of the genotypes were represented by one individual, we employed the Roff and Bentzen (1989) Monte Carlo approach to estimate the significance of heterogeneity χ^2 values determined from the raw data.

Results

The analysis of 472 mid-Atlantic bluefish with 9 restriction endonucleases revealed 40 mtDNA genotypes, and 2 mtDNA genotypes were encountered among 19 Australian bluefish. A total of 77 restriction fragments was visualized, and the average individual was scored for 34 fragments, accounting for approximately 1.4% of the mtDNA genome. The restriction endonucleases, *Hin*dIII and *Pst*I, revealed no variant fragment patterns, while the remaining seven enzymes revealed from two (*Sst*I and *Sst*II) to eight (*Nci*I) different fragment patterns. Restriction-site gains or losses were inferred from completely additive changes in fragment patterns.

Considerable RFLP variation was detected within Atlantic bluefish samples (Table 2). The most common mtDNA genotype, AAAAAAAAA, ranged in frequency from 0.43 (NC 1990 YOY) to 0.75 (NJ 1990 YOY). The large number of variant genotypes resulted in nucleon diversities ranging from 0.416 to 0.798 (Table 3). Because many of the variant genotypes differed from the common genotype by several site changes, the within-sample mean nucleotide sequence diversities were also relatively high, varying from 0.63% to 1.49%. In contrast to the mid-Atlantic bluefish, the Australian sample was quite depauperate of variation. Of the 19 fish in the sample, 18 shared a common mtDNA genotype (AAAEEAAAD), and one fish had a genotype differing from the common type by a single site change (Table 2). The lack of variation in the Australian sample was reflected in a low nucleon diversity (0.105) and a within-sample mean nucleotide sequence diversity of 0.07%.

Significant genetic differentiation was not found between the samples of spring- and summer-spawned YOY bluefish collected in New Jersey during the summer of 1990. The corrected mean nucleotide sequence divergence between the two samples was extremely small (0.02%), indicating that average sequence divergence between two individuals randomly drawn from either the spring- or summer-spawned sample was the same as the divergence between two individuals randomly drawn from each group.

Table 3

Genetic variation within bluefish *Pomatomus saltatrix* samples expressed as nucleon diversity and mean nucleotide sequence diversity. The spring- and summer-spawned NJ YOY bluefish collections were pooled (NJ90 combined) for comparison with the NC90 YOY sample, and all NJ, VA, and NC bluefish collections were pooled (mid-Atlantic combined) for comparison with the AU91 YOY sample. YRL = yearling; YOY = young-of-the-year.

Sample	Age	n	Nucleon diversity	Mean nucleotide sequence diversity
VA88	YRL	100	0.781	1.34%
VA89	YRL	102	0.777	1.41%
VA90	YRL	36	0.565	0.89%
NC88	YRL	83	0.632	1.15%
NC89	YRL	57	0.663	1.20%
NJ90-Sp	YOY	26	0.416	0.72%
NJ90-Su	YOY	25	0.467	0.63%
NJ90 combined	YOY	51	0.438	0.67%
NC90	YOY	40	0.798	1.49%
mid-Atlantic combined		372	0.696	1.23%
AU91	YOY	19	0.105	0.07%

Considerable genetic differentiation was not detected among samples of yearling bluefish collected at the same site in different years. The mean nucleotide sequence divergences (Table 4) among the VA88, VA89, and VA90 collections, and between the NC88 and NC90 samples, were of the same magnitude as the within-sample mean nucleotide sequence diversities (Table 3). Consequently, when adjusted for within-sample diversity (Nei 1987), the corrected mean nucleotide sequence divergences among samples were nearly zero (Table 4).

Table 4

Mean nucleotide sequence divergences (%) among selected bluefish *Pomatomus saltatrix* collections. Values are presented with and without correction for within-sample variation.

Collections	Uncorrected	Corrected
Among collections at a single location over 2 or more years		
VA88 vs. VA89	1.39	0.11
VA88 vs. VA90	1.20	0.18
VA89 vs. VA90	1.20	0.05
NC88 vs. NC89	1.18	0.01
Between spring- and summer-spawned bluefish		
NJ90-Sp vs. NJ90-Su	0.69	0.02
Between mid-Atlantic YOY fish		
NJ90-combined vs. NC90	1.19	0.11
Between mid-Atlantic and Australian bluefish		
mid-Atlantic combined vs. AU91	2.60	1.96

Analysis of YOY bluefish from the northern and southern mid-Atlantic bight revealed little mtDNA genetic differentiation. The corrected mean nucleotide sequence divergence between the combined NJ90 YOY sample and the NC90 YOY collection was 0.11%, suggesting little population structuring along the mid-Atlantic coast. This inference was further supported by an analysis of heterogeneity which demonstrated no significant differences in the distribution of six major mtDNA genotypes (those occurring in 10 or more of the 472 fish) and the pooled rare genotypes among the seven mid-Atlantic collections ($G_H = 39.5$, $0.25 < P < 0.50$). Heterogeneity χ^2 analysis of the distribution of all genotypes, including those represented by a single individual, was performed using the Monte Carlo simulation of Roff and Bentzen (1989). A total of 320 of the 1000 randomizations produced χ^2 values greater than the original data set, indicating no significant heterogeneity.

The low levels of mtDNA differentiation among mid-Atlantic bluefish collections contrasted with the substantial difference encountered between the combined mid-Atlantic bluefish and the Australian sample. The average mid-Atlantic bluefish could be distinguished from its Australian conspecific by three or more restriction-site changes. Two of the site changes were unique to the Australian sample, and the third (*Nci*I pattern D) occurred at a low frequency (0.01) in the combined mid-Atlantic sample. The corrected mean nucleotide sequence divergence between the Australian sample and the combined mid-Atlantic bluefish samples was 1.95%. Significant heterogeneity was noted among the pooled samples when the Australian sample was included with the mid-Atlantic bluefish ($G_H = 177$, $p < 0.001$).

A sample of 10 yearling bluefish was analyzed from the northeast Gulf of Mexico (Panama City, FL). Unlike the Australian bluefish, all of the mtDNA genotypes found in the Gulf of Mexico mtDNA individuals were also present in the mid-Atlantic samples, and 7 of the 10 Gulf of Mexico bluefish had the common mid-Atlantic mtDNA genotype. Because of the small size of the Gulf of Mexico sample, it was not appropriate to test for frequency differences between bluefish from the mid-Atlantic coast and the Gulf of Mexico.

Discussion

Mid-Atlantic bluefish demonstrated considerable mtDNA genotypic variation. It is difficult to directly compare the nucleon diversities calculated in this study with those from other studies because the value is sensitive to the number of restriction sites surveyed, and analyses employing larger numbers of restriction endonucleases typically have higher nucleon diversities. The value of 0.696 for the pooled mid-Atlantic bluefish samples is higher than those reported for many marine fishes surveyed with a larger number of enzymes (Avise et al. 1989, Gold and Richardson 1991), and indicates a relatively high degree of genetic variation within the bluefish. This trend becomes more apparent when mean nucleotide sequence diversities, a measure of intrasample diversity that is much less sensitive to the number of restriction sites surveyed, are compared. The value calculated in this study for the pooled mid-Atlantic samples, 1.23%, is higher than values reported for many other marine fishes (Ovenden 1990).

The Australian bluefish demonstrated much less variation than their mid-Atlantic conspecifics. The sample of 19 Australian bluefish had a nucleon diversity five times lower than the combined Atlantic samples, and a mean nucleotide sequence diversity that was an order of magnitude lower (Table 3). A similar difference in the level of mtDNA variation between

conspecific populations has been noted between Atlantic and Pacific blue marlin (Graves and McDowell, unpubl. data). The striking lack of variation within the Australian sample could be the result of a smaller effective population size of females resulting from population bottlenecks, or may simply reflect a period of isolation sufficient for the sorting of gene trees (Nei 1987, Avise et al. 1988, Chapman 1990, Bowen and Avise 1990).

We found little evidence to support the hypothesis that genetically distinct stocks of bluefish exist along the mid-Atlantic coast. Although appreciable mean nucleotide sequence divergences were found between sampling locations (Table 4), when corrected for within-group variation the values became extremely small, indicating that most of the observed differentiation could be accounted for by variation within the samples. The lack of population structuring was also supported by the homogeneous distribution of all genotypes and the fact that the level of genetic divergence among sampling locations was not appreciably greater than the level of divergence among samples taken at any one location in different years.

The extent of gene flow among populations can also be inferred from the frequency distribution of rare alleles (Slatkin 1989). An inspection of Table 2 indicates that almost all mtDNA genotypes that occurred more than once were found in different collections, suggesting significant gene flow among sampling locations. For example, the genotype AAAABAABA, which was present in three individuals, occurred in the VA89, NC88, and NJ90-Su collections. An exception to this pattern was presented by the genotype AAAAAAAAD, which occurred seven times: in six individuals of the VA88 sample and one individual of the VA89 sample. However, an examination of bluefish mtDNA genotypes not included in this analysis—because the individuals were greater than one year old, or because they came from a sample that was too small for inclusion in this analysis—suggests that the observed distribution of the AAAAAAAAD genotype may be an artifact of sampling error. The genotype was present in two bluefish collected in 1988 (one in New York and one in Connecticut) and in six bluefish collected in 1989 (two in New York, two in Virginia, and two in North Carolina).

In contrast to the genetic similarity among mid-Atlantic samples, a large, consistent genotypic difference was noted between the mid-Atlantic bluefish and a conspecific population in Australia. The corrected mean nucleotide sequence divergence of almost 2% is more than an order of magnitude larger than the values detected among mid-Atlantic samples, and is similar to values reported between northwest Atlantic and Barents Sea capelin populations (Dodson et al. 1991) or among populations of freshwater fishes of different river systems (Bermingham and Avise 1986).

While significant genetic differentiation was found between mid-Atlantic and Australian bluefish, no major differences were detected between mid-Atlantic bluefish and a small sample from the Gulf of Mexico. Consistent restriction-site differences have been reported between Gulf of Mexico and mid-Atlantic populations of a number of marine organisms, including horshoe crabs *Limulus polyphemus* (Saunders et al. 1986), oysters *Crassostrea virginica* (Reeb and Avise 1990), and black sea bass *Centropristis striata* (Bowen and Avise 1990). These preliminary results suggest that bluefish from the Gulf of Mexico and the mid-Atlantic are not as genetically isolated as many other coastal marine species, although much larger samples will have to be surveyed to determine if significant mtDNA genotypic frequency differences exist between the two areas. Considering the high vagility of bluefish and their continuous distribution around Florida, this result is not unexpected.

The lack of significant genetic differentiation between spring- and summer-spawned bluefish is consistent with the results of Chiarella and Conover (1990), who found no correlation between the season in which an adult bluefish spawned and the hatch-date of an individual. These data suggest that the bimodal distribution of YOY bluefish in mid-Atlantic estuaries results from two major spawning events of the same population of bluefish, rather than the participation of different stocks. The morphological differences found between spring- and summer-spawned bluefish are probably ecophenotypic, resulting from early-life-history development in appreciably different environments. Similar morphological plasticity has been demonstrated in many other marine fishes (Barlow 1961).

The high degree of genetic homogeneity detected within mid-Atlantic bluefish is also consistent with the results of tag and recapture studies. While many bluefish return to the same site for several years (Lund and Maltezos 1970), migratory habits appear to change with age (Wilk 1977). Thus, the potential exists for considerable interchange, and it is important to note that even small levels of exchange can prevent the accumulation of genetic differentiation (Hartl 1988).

The results of this study cannot disprove the null hypothesis that bluefish along the mid-Atlantic coast share a common gene pool. There appears to be sufficient gene flow to prevent the accumulation of even slight genetic differences. Determining the magnitude of exchange between geographic regions would require an extensive tag and recapture program. Until such data are available, the resource should be managed as assumed in the Fishery Management Plan for the Bluefish—as a single, genetically homogeneous stock.

Acknowledgments

Bluefish were kindly provided by Hunt Howell, Alice Webber, Raoul Castaneda, Bill Andrews, Katy West, Debbie Fabel, Steve Battaglane, and R. Bill Talbot. This project resulted from a study initiated by Herb Austin and Brian Meehan of the Virginia Institue of Marine Science. Robert Chapman provided helpful advice with the statistical analysis. Critical reviews of the manuscript were provided by John Olney and John Musick. Funding for this research was provided by the U.S. Fish and Wildlife Service (F-60-R) and the Commonwealth of Virginia.

Citations

Avise, J.C., R.M. Ball, and J. Arnold
1988 Current versus historical population sizes in vertebrate species with high gene flow: A comparison based on mitochondrial DNA lineages and inbreeding theory for neutral mutations. Mol. Biol. Evol. 5:331–344.

Avise, J.C., B.W. Bowen, and T. Lamb
1989 DNA fingerprints from hypervariable mitochondrial genotypes. Mol. Biol. Evol. 6:258–269.

Barlow, G.W.
1961 Causes and significance of morphological variation in fishes. Syst. Zool. 10:105–117.

Bermingham, E., and J.C. Avise
1986 Molecular zoogeography of freshwater fishes in the southeastern United States. Genetics 113:939–965.

Bowen, B.W., and J.C. Avise
1990 Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: Influence of zoogeographic factors and life-history patterns. Mar. Biol. (Berl.) 107:371–381.

Briggs, J.C.
1960 Fishes of world-wide (circumtropical) distribution. Copeia 1960:171–180.

Chapman, R.W.
1990 Mitochondrial DNA analysis of striped bass populations in Chesapeake Bay. Copeia 1990:355–366.

Chapman, R.W., and D.A. Powers
1984 A method for the rapid isolation of mitochondrial DNA from fishes. Tech. Rep. UM-SG-TS-84-01, Md. Sea Grant Prog., Univ. Md., College Park, 11 p.

Chiarela, L.A., and D.O. Conover
1990 Spawning season and first-year growth of adult bluefish from the New York bight. Trans. Am. Fish. Soc. 119:455–462.

Collins, M.R., and B.W. Stender
1988 Larval king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States, 1973–1980. Bull. Mar. Sci. 41:822–834.

Dodson, J.J., J.E. Carscadden, L. Bernatchez, and F. Colombani
1991 Relationship between spawning mode and phylogeographic structure in mitochondrial DNA of north Atlantic capelin *Mallotus villosus*. Mar. Ecol. Prog. Ser. 76:1103–113.

Gold, J.R., and L.R. Richardson
1991 Genetic studies in marine fishes. IV. An analysis of population structure in the red drum (*Sciaenops ocellatus*) using mitochondrial DNA. Fish. Res. 12:213–241.

Hartl, D.L.
1988 A primer of population genetics. Sinauer Assoc., Sunderland, MA, 305 p.

Kendall, A.W. Jr., and L.A. Walford
1979 Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull., U.S. 77:213–227.

Lansman, R.A., R.O. Shade, C.F. Shapira, and J.C. Avise
1981 The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. III. Techniques and potential applications. J. Mol. Evol. 17:214–226.

Lassiter, R.R.
1962 Life history aspects of the bluefish fish, *Pomatomus saltatrix* Linnaeus, from the coast of North Carolina. Master's thesis, N.C. State College, Raleigh, 103 p.

Lund, W.A. Jr., and G.C. Maltezos
1970 Movements and migrations of the bluefish, *Pomatomus saltatrix*, tagged in waters of New York and southern New England. Trans. Am. Fish. Soc. 99:719–725.

Maniatis, T., I.F. Fritsch, and J. Sambrook
1982 Molecular cloning: A laboratory manual. Cold Spring Harbor Lab., Cold Spring Harbor, NY, 545 p.

McBride, R.S.
1989 Comparative growth and abundance of spring versus summer-spawned juvenile bluefish, *Pomatomus saltatrix*, recruiting to New Youk bight. Master's thesis, State Univ. New York, Stony Brook, 61 p.

Nei, M.
1987 Molecular evolutionary genetics. Columbia Univ. Press, NY, 512 p.

Nei, M., and W-H. Li
1979 Mathematical model for studying genetic variation in terms of restriction endonucleases. Proc. Natl. Acad. Sci. 76:5269–5273.

Nyman, R.M., and D.O. Conover
1988 The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. Fish. Bull., U.S. 86:237–250.

Ovenden, J.R.
1990 Mitochondrial DNA and marine stock assessment: A review. Aust. J. Mar. Freshwater Res. 41:835–53.

Reeb, C.A., and J.C. Avise
1990 A genetic discontinuity in a continuously distributed species: Mitochondrial DNA in the American oyster, *Crassostrea virginica*. Genetics 124:397–406.

Roff, D.A., and P. Bentzen
1989 The statistical analysis of mitochondrial DNA polymorphisms: χ^2 and the problem of small samples. Mol. Biol. Evol. 6:539–545.

Saunders, N.C., L.G. Kessler, and J.C. Avise
1986 Genetic variation and geographic differentiation in mitochondrial DNA of the horshoe crab, *Limulus polyphemus*. Genetics 112:613–627.

Slatkin, M.
1989 Gene flow and the geographic structure of natural populations. Science (Wash. DC) 236:787–792.

Smith, J.L.B.
1949 The sea fishes of southern Africa. Central News Agency, Cape Town, 550 p.

Sokal, R.R., and F.J. Rohlf
1981 Biometry. W.H. Freeman, NY.

Wilk, S.J.
1977 Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Tech. Ser. Rep. 11, Sandy Hook Lab., NMFS Northeast Fish. Sci. Cent., Highlands, NJ, 56 p.

Abstract. – Age, growth, and mortality of larval Atlantic bumper *Chloroscombrus chrysurus* were compared between cruise samples collected during August–September 1986 and September 1987 off the Louisiana–Mississippi barrier islands. Calcein-marked Atlantic bumper otoliths (sagitta) were used for age validation. The first growth increment formed on the sagitta approximately 2 days after spawning, and daily increments formed thereafter. Length at hatching was estimated at 0.7–0.9 mm SL. Growth rates were determined from sagitta and length-frequency data. Highest growth rates occurred in August 1986 (0.40 mm/day) and were associated with highest mean temperature and zooplankton standing stock estimates. The length exponent for Atlantic bumpers' dry weight-length relationship was 3.25. Instantaneous daily mortalities (M) ranged from 0.62 in August 1986 to 0.17 in late September 1987.

Manuscript accepted 1 July 1992.
Fishery Bulletin, U.S. 90:711–719 (1992).

Age validation, growth, and mortality of larval Atlantic bumper (Carangidae: *Chloroscombrus chrysurus*) in the northern Gulf of Mexico

Deborah L. Leffler

Florida Marine Research Institute, Florida Department of Natural Resources
3 Jackson Street, Fort Walton Beach, Florida 32548

Richard F. Shaw

Coastal Fisheries Institute, Center for Wetland Resources
Louisiana State University, Baton Rouge, Louisiana 70803-7503

Atlantic bumper *Chloroscombrus chrysurus*, a carangid, is an abundant coastal pelagic fish that is widely distributed in the western Atlantic and Gulf of Mexico (Leak 1977). Exploratory fishing surveys indicate that Atlantic bumper may be abundant enough in the northern Gulf of Mexico to harvest commercially (Juhl 1966, Bullis and Carpenter 1968, Bullis and Thompson 1970, Klima 1971). Presently, Atlantic bumper is mainly a commercial bycatch, marketed primarily for petfood, with little potential as a food fish in the United States (Klima 1971, Leak 1977). It, however, may be an important food source for many predatory fish (Reintjes 1979).

Atlantic bumper spawn primarily in nearshore coastal waters, especially off Louisiana and Mississippi (Boschung 1957, Perret et al. 1971, Christmas and Waller 1973, Ditty 1986, Shaw and Drullinger 1990), and the larvae of this species were most abundant during surveys off the Louisiana–Mississippi (LA–MS) barrier islands (Stuck and Perry 1982, Leffler 1989). Larvae have been collected from June to October, with abundance peaks usually occurring in July or August (Sabins 1973, Stuck and Perry 1982, Williams 1983, Ditty 1986).

Very little early-life-history work has been conducted on Atlantic bumper (Shaw and Drullinger 1990). Early-life-history information is a critical component in estimating future year-class strength (Cushing 1975, Leak and Houde 1987). For example, slow larval growth rates influence mortality by extending the duration of vulnerable larval stages (Bannister et al. 1974, Houde 1987), while a fast growth rate can possibly increase interaction with predators (Pepin 1991), thereby influencing recruitment. Early-life-history data are needed for Atlantic bumper to determine their ecological role and to assist in the prudent development of any directed fishery.

The abundance of Atlantic bumper over a wide geographic range, their perceived potential as a commercial resource, and their probable ecological importance as a forage fish, provided the impetus for conducting this larval age-and-growth study. The goals of this ichthyoplankton study were to (1) validate the periodicity of growth increments on larval and juvenile Atlantic bumper otoliths, (2) estimate Atlantic bumper length at hatching, (3) estimate the age structure of the sample population, (4) describe larval growth and mortality rates, and (5) relate larval growth

and mortality rates to environmental parameters and food availability.

Materials and methods

Sampling procedure

Atlantic bumper larvae were collected during five cruises off the Louisiana–Mississippi barrier islands in the Gulf of Mexico (Chandeleur Is., Ship I., and Horn I.; 29°50′–30°15′N and 88°40′–89°00′W; Fig. 1). Three cruises were completed in 1986 (5–7 Aug., 8–9 Sept., and 22–24 Sept.) and two in 1987 (8–10 and 24–26 Sept.). Adverse weather conditions canceled the scheduled August 1987 cruise.

The sampling design consisted of a 4×4 grid of stations (N 16) randomly sampled on two consecutive nights, and a 3×3 grid of stations (N 9) randomly sampled during daylight, starting 12 hours after the initiation of the first nocturnal sampling. The sampling grid had a fixed compass orientation with respect to three windowshade, subsurface current drogues (five drogues were used in 1987) which were released at the beginning of each cruise (Shaw et al. 1988). The change to five drogues in 1987 allowed for a more defined sampling grid. Surface-water temperature and salinity, as well as water depth, were recorded for each ichthyoplankton tow.

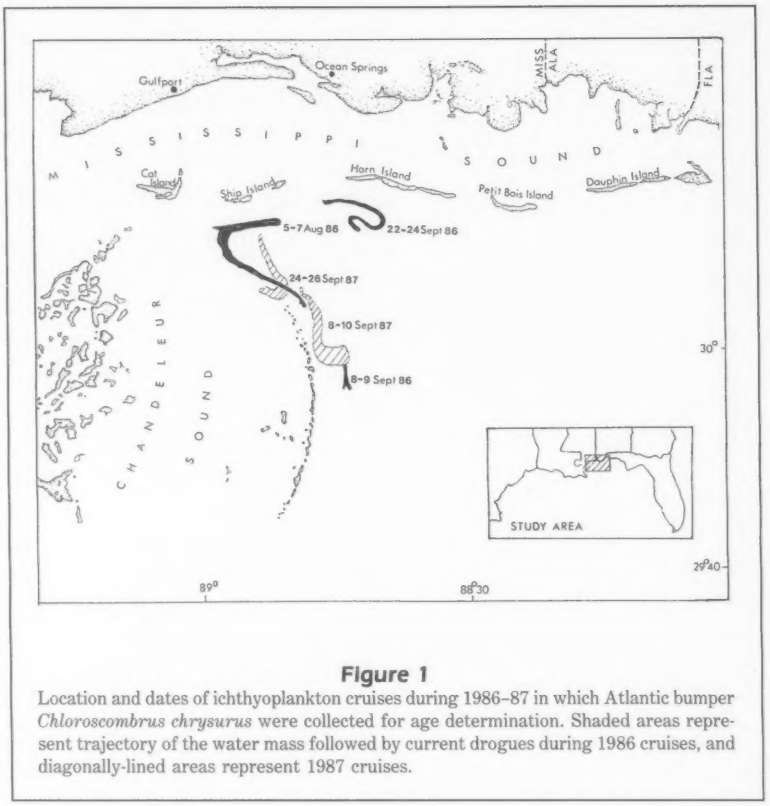


Figure 1

Location and dates of ichthyoplankton cruises during 1986–87 in which Atlantic bumper *Chloroscombrus chrysurus* were collected for age determination. Shaded areas represent trajectory of the water mass followed by current drogues during 1986 cruises, and diagonally-lined areas represent 1987 cruises.

Three-minute surface tows were taken at ~1.0 m/s using a 60 cm "bongo-type" plankton sampler fitted with a flowmeter (General Oceanics model 2030). In 1986, samples were collected using a 202 μm mesh net, while in 1987 a 333 μm mesh net was used. During the two cruises in September 1987, the bongo sampler was fitted with one 202 μm mesh net and one 333 μm mesh net for comparisons of daytime collections. Atlantic bumper collected using the two mesh sizes were placed into 1 mm size-classes and tested for differences using a Median test (α 0.05; SAS Inst. 1985). Ichthyoplankton samples used for age determination were preserved with 95% ethanol, stored in ice water, and later transferred to 70% ethanol in the lab.

Live larval and juvenile Atlantic bumper were collected for an age-validation experiment and length-weight measurement analysis by dipnetting the jellyfish *Aurelia aurita* with which the fish are often associated (Reid 1954, Franks 1970). Fish were then transferred to a cooler containing 100 ppm calcein (2,4-bis-[N,N′-di(carbomethyl)aminomethyl]fluorescein) in 13 L of aerated ambient seawater to create a fluorescent mark in their otoliths using the method described by Wilson et al. (1987). Fish were held between 6 and 12 h in the seawater-calcein solution and then transferred into a 127 L aquaria. Fish were held under a 12h/12h photoperiod in 23°C and 25 ppt water and fed *ad libidium* on brine shrimp. Fish were sacrificed 2, 7, and 10 days after marking.

Lab analysis

Ichthyoplankton samples from the bongo net collections were split once with a Folsom plankton splitter (Van Guelpin et al. 1982). *Chloroscombrus chrysurus* larvae were sorted, counted, and measured to the nearest 0.1 mm standard length (SL). Preflexion larvae were measured to the end of their notochord, otherwise larvae were measured to the posterior tip of the hypural plate. When more than 52 fish were present,

a random subsample of 50 fish were measured, as well as the shortest and longest. Ethanol-related shrinkage was assumed to be uniform for each fish collected and preserved (3-min tow, alcohol preservation; see Radtke 1989).

Validation, age, and growth

Sagittal otoliths were removed from each Atlantic bumper larvae using a dissection microscope equipped with polarized light. The sagitta from nine postlarval and juvenile Atlantic bumper (8.3–25.0 mm SL) that were immersed in the calcein-seawater solution were prepared and viewed using the method described by Wilson et al. (1987). Growth increments, following the fluorescent mark, were counted at 400× and verified at 1000×. The number of growth increments counted from the calcein mark to the otolith edge were compared with the number of days fish were held in captivity after marking.

Age estimation of larval Atlantic bumper was performed using sagitta that were air-dried and mounted in S/P Accu-mount 60 on a glass microscope slide. Most larval otoliths were thin enough that only viewing under a compound microscope was necessary to make total increment counts and otolith radius measurements. A few larger otoliths were ground with 600 WetorDry grit sandpaper and polished using 0.3μ Alumina 2 Alpha Micropolish until growth rings were countable. The counting and measurement procedure was enhanced by using a digital imaging system which produced images on a video monitor at 400× or 1000×. Independent increment counts were made twice by the same person without knowledge of fish length or previous otolith count. Only otoliths for which replicate counts were identical were used in the analysis. Eleven of the 170 otoliths prepared were discarded.

Separate linear growth equations of standard length on increment number were developed for fishes collected on the five cruises. These five equations were compared using analysis of covariance (ANCOVA, α 0.05; SAS Inst. 1985). Exponential and other nonlinear models (e.g., Laird-Gompertz) used to describe larval growth were also tested (Campana and Neilson 1985). A General Linear Model ANOVA, followed by a multiple comparisons test (Duncan, α 0.05; SAS Inst. 1985), were used to detect differences in surface-water temperature between years, months, and cruises.

Zooplankton biomass

Zooplankton displacement volumes (mL/m^3) were determined (Yentsch and Hebard 1957) for each net tow. A mean zooplankton standing stock value was then calculated for each cruise and net mesh type. A simple regression of zooplankton standing-stock values (202 vs. 333μm mesh nets) was developed for both September 1987 cruises. ANCOVA (α 0.05) was used to test for differences between the two cruises. The data from the two cruises were combined into one zooplankton standing-stock regression to standardize the values from the two mesh sizes.

Dry weight-length relationship

Larval and juvenile Atlantic bumper (N 120, 8.0–32.0 mm SL) collected by dipnetting for jellyfish, were measured to the nearest 0.1 mm SL, oven dried for 6 h at 62°C, and then weighed to the nearest 1.0 mg. A log-log dry weight-length relationship was established and described by the equation $W = aL^b$, where $W = \log_{10}$ dry weight (mg), and $L = \log_{10}$ standard length (mm). A 95% confidence interval placed around the estimated slope (b) was used to test for differences in the estimated length power term (b) and the classical b estimate of 3.0 for adult fish (LeCren 1951) and 4.0 for larval fish (Power 1989).

Mortality

Atlantic bumper densities for each 1 mm SL category were converted into mortality estimates following the length-frequency method described by Essig and Cole (1986). Sampling with respect to the windowshade drogues allowed us to monitor larval densities from the same mass of water for an entire collecting period. Only nighttime collected larvae >2.0 mm or <5.0 mm were utilized in our mortality estimates to minimize biases from net avoidance by larger larvae or extrusion through the mesh openings by the smallest larvae. The descending limb of each age-frequency distribution corresponding to a length range of 2.0–5.0 mm SL was described by the equation $Dt = Do\exp^{(-Mt)}$, where M = the instantaneous daily mortality coefficient, Dt = larval fish density at time t, Do = larval fish density in the first fully recruited group (i.e., time = 0), and t = time in days (Peebles and Tolley 1988). Mortality estimates were tested for statistical differences between cruises and years using ANCOVA (α 0.05).

Results

Validation, age, and growth

Daily increment formation on Atlantic bumper sagitta was validated using calcein. Each otolith from the nine fish treated had distinct growth increments between the green fluorescent calcein mark and the edge of the otolith (Fig. 2). On each sagitta examined, the number of increments counted after the calcein mark was

Figure 2
Photomicrograph (400×) of the transverse-sectioned sagittal otolith of a 23.5 mm SL juvenile Atlantic bumper *Chloroscombrus chrysurus* observed under ultraviolet light. The lower light band displays the uptake of calcein during the immersion process.

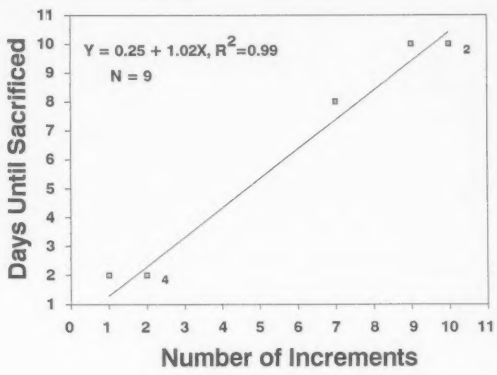


Figure 3
Regression of the number of otolith growth increments subsequent to the fluorescent calcein mark on the number of days each fish was held in captivity before sacrificing. Numbers associated with points represent overlapping values.

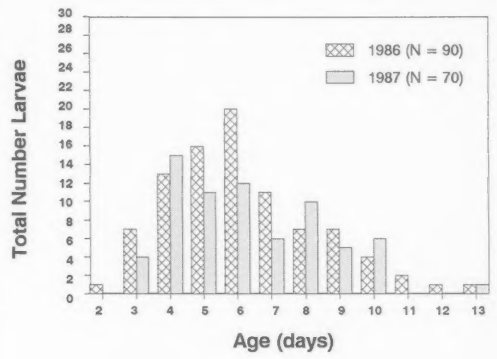


Figure 4
Age distribution of Atlantic bumper *Chloroscombrus chrysurus* larvae captured off the Louisiana–Mississippi barrier islands, 1986–87.

equivalent to the number of days the fish was held in captivity. The slope (1.02) of a least-squares linear regression (Fig. 3) was not significantly different from 1.0 (t-test, $p>0.05$), confirming daily increment formation in otoliths of larval and juvenile Atlantic bumper.

Larval Atlantic bumper have circular sagitta, with a central core. Yolksac larvae (0.8 mm SL, preserved length) lacked increments. However, all other aged fish between 1.0 and 5.0 mm (preserved length; N 158) had countable increments (i.e., 1–11 increments or 3–13 days old; Fig. 4). Growth models were based only on 2–13 day-old fish.

Larval Atlantic bumper growth rates during the first two weeks of life were best described using a linear model. A separate growth curve was estimated for the 5–7 August 1986 data (Table 1). Growth curve comparisons for the two cruises in September 1986 (days 8–9 and 22–24) showed no significant differences within month (intercept, p 0.44; slope, p 0.48). Similarly, no significant difference was found between the two September cruises in 1987 (days 8–10 and 24–26; intercept, p 0.07; slope, p 0.42). Therefore, the paired September data sets were combined into a single regression for each year (1986 and 1987; Table 1). Atlantic bumper length-frequencies displayed no significant differences (p 0.93) between the two different mesh sizes (202 vs. 333 μm) during the 1987 daytime

Table 1

Estimates of three linear growth equations used to describe the growth rate (mm/day) of larval *Chloroscombrus chrysurus* (0.8–4.8 mm) collected off the Louisiana–Mississippi barrier islands during 1986 and 1987, and the associated mean surface-water temperatures (°C) including ranges. R^2 is the coefficient of determination for the respective models; L = standard length (mm); X = age (days).

Sampling date	Number fish aged	Size (range)	Equations	R^2	Growth rate (mm/day)	Mean surface-temperature (°C) (range)
5–7 August 1986	9	0.8–3.7	L=0.40X−0.13	0.94	0.40	29.6 (29.0–30.8)
8–9, 22–24 Sept. 1986	81	1.2–4.8	L=0.26X+0.70	0.61	0.26	28.4 (28.0–29.0)
8–10, 24–26 Sept. 1987	69	1.3–4.5	L=0.31X+0.71	0.72	0.31	27.8 (26.5–30.0)

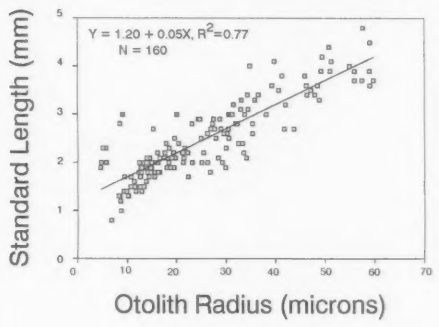


Figure 5

Regression of larval standard length (mm) on sagittal otolith radius (μ) for Atlantic bumper *Chloroscombrus chrysurus* larvae collected off the Louisiana–Mississippi barrier islands, 1986–87.

Table 2

Zooplankton standing-stock estimates (mL/m³ ± SE) with 1987 values converted to equivalent 202 μm mesh net values, based on the conversion study done during both September cruises in 1987. The number of samples taken during each cruise is indicated in parentheses. The following equation was used in the conversion: Y = 0.785X − 0.054 (R^2 0.86).

	1986	1987	
Month	(202 μm)	Converted	(333 μm)
August	0.83 ± 0.17 (34)	—	—
early Sept.	0.61 ± 0.13 (25)	0.57 ± 0.04 (40)	0.39 ± 0.04 (40)
late Sept.	0.32 ± 0.05 (41)	0.39 ± 0.03 (40)	0.25 ± 0.03 (40)

collections. Comparisons of the growth curves for September 1986 and 1987 and August 1986 indicated a significant difference in both the August intercept ($p<0.04$) and slope ($p<0.03$) of the regressions. Even though the sample size (N 9) was small, the observed growth rate for August (0.40 mm/day) was significantly higher than for September (0.26 mm/day in 1986 and 0.31 mm/day in 1987). The higher August growth rate occurred at a higher mean surface-water temperature, 29.6°C (Table 1). In September of 1987, the water temperature range (26.5–30.0°C) was wider than the other sampling periods due to a cold front passing through before the late-September cruise. There was, however, no significant difference (p 0.11) in temperature between months because of the low number of cruises.

Atlantic bumper standard lengths were regressed on the otolith radius (measured in microns; Fig. 5). The coefficient of determination (r^2) for the relationship was 0.77 and the equation is L = 120 + 0.05R, where L = standard larval length (mm) at the otolith radius, R (Fig. 5). The relationship between the age and otolith radius explained less variability (r^2 0.68) and fit the following equation A = 2.96 + 0.13R, where A = age in days at the otolith radius, R. Otolith radius was observed to increase with both larval length and age.

Zooplankton biomass

Zooplankton mean biomass values for 1986 were similar to the converted 1987 values. The 202 vs. 333 μm mesh regression equation Y = −0.054 + 0.785X (r^2 0.86), where Y = the 333 μm zooplankton standing-stock value, and X = the 202 μm zooplankton value, was used to establish a correction factor to convert the 1987 zooplankton values into estimates comparable to the 1986 values. The highest mean zooplankton biomass estimate (0.83 mL/m³) was found in August 1986 (Table 2). The mean standing-stock estimates declined throughout the September cruises within each year (Table 2).

Dry weight-length relationship

The dry weight-length relationship for postlarval and juvenile Atlantic bumper (Fig. 6) is described by the exponential model Weight = 0.0016 Length$^{3.25}$ (r^2 0.94), where weight = dry weight of the fish (mg) and length = standard length (mm). The dry weight-length power term for larval and juvenile Atlantic bumper, 3.25, is significantly different from the classical standard length-weight power term of 3.0 for adult fish (LeCren 1951) and 4.0 for larval fish (Power 1989) at the 95% confidence level ($p>0.05$).

Mortality

Instantaneous daily mortality (M) for larval Atlantic bumper was significantly higher during August 1986 (F 13.8, p 0.03) than in either September 1986 or 1987, with September values decreasing during successive cruises each year (Table 3). As a whole, however, the M values for all cruises in 1986 and 1987 were similar (F 0.74, p 0.45).

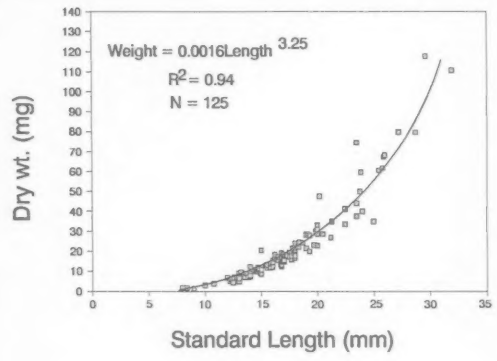


Figure 6
Relationship between dry weight and standard length of Atlantic bumper *Chloroscombrus chrysurus* collected off the Louisiana–Mississippi barrier islands, 1986–87.

Discussion

The age of larval and juvenile Atlantic bumper was estimated from counts of growth increments on sagittal otoliths. One growth increment formed daily on each sagitta of Atlantic bumper between 8 and 25 mm SL. We, like others (Pritcher 1988, Fowler 1989, Parsons and Peters 1989), assumed that this relationship held true for smaller larvae (1–8 mm). We validated the periodicity of otolith growth increments and established an otolith age-and-growth analysis for larval Atlantic bumper in the northern Gulf of Mexico.

Growth increments were not visible in the otoliths of yolksac Atlantic bumper larvae (0.8 mm NL), but at least one increment was visible in 1.0 mm SL larvae. The length at hatching appears to be between 0.7 and 0.9 mm SL (after preservation) based on the larval length measurements. Atlantic bumper larvae, therefore, appear to begin otolith increment deposition after yolksac absorption, approximately 2 days after spawning (allowing 1 day each for egg incubation and yolksac absorption). Pelagic species, such as Atlantic bumper, often begin growth increment formation on their sagitta at the time of yolksac absorption (Radtke 1984).

An isometric or linear relationship between the size of otolith radius and standard length was revealed for Atlantic bumper larvae. The variation observed in our otolith radius–fish size relationship could be influenced by growth- and age-related factors. For example, under unfavorable environmental conditions the fish may not continue to experience an increase in otolith radius or fish size, while daily increment formation may continue (Lyczkowski-Shultz et al. 1988, Secor and Dean 1989).

Table 3
Estimates of instantaneous daily mortality of larval *Chloroscombrus chrysurus* (2.0–5.0 mm SL) off the Louisiana–Mississippi barrier islands were calculated using the length-frequency method. Total larval Atlantic bumper densities and total larval fish densities were included for each cruise in 1986 and 1987. R^2 is the coefficient of determination for the respective models.

Sampling dates	Number of fish	Instantaneous daily mortality estimates (M)	R^2	Atlantic bumper total densities (# fish/100 m^3)	Total larval fish density (# fish/100 m^3)
5–7 August 1986	1912	0.62	0.82	608.9	1838.1
8–9 Sept. 1986	576	0.35	0.98	121.7	799.8
22–24 Sept. 1986	291	0.18	0.86	227.9	599.9
8–10 Sept. 1987	573	0.30	0.90	62.2	262.4
24–26 Sept. 1987	122	0.17	0.92	42.4	298.2

Temperature (Laurence 1978, Laurence et al. 1981, Houde 1989) and food availability (Methot and Kramer 1979, Laurence et al. 1981, Lyczkowski-Shultz et al. 1988, Warlen 1988) play important roles in larval growth and survival. Atlantic bumper growth rates were highest in August 1986, when mean surface-water temperatures and zooplankton biomass estimates were greatest.

The Atlantic bumper growth rate calculated over the two cruises in September 1987 may have been higher than the September 1986 growth rate because of the increase in zooplankton availability (Tables 1 and 2). Zooplankton displacement volume values calculated from the samples taken in 1986 declined from August to September. Relative zooplankton biomass values have peaked, however, as late as October off the Chandeleur Is. within Chandeleur Sound (102,000 animals/100 m^3; Gillespie 1971; Fig. 1). Our zooplankton standing-stock estimates were high compared with values obtained from Mississippi River plume fronts during July 1987 (0.04–0.43 mL/m^3; R.F. Shaw, unpubl. data).

Atlantic bumper larvae had a dry weight-length exponent value of 3.25 which is similar to that of 3.32 determined for larval northern anchovy *Engraulis mordax* (Lasker et al. 1970). This power term, however, is lower than values determined for seven laboratory-reared, cold-water marine larval species (3.76–4.77; Laurence 1979), or the hypothesized standard value for developing larval fish (4.0; Power 1989).

The highest Atlantic bumper instantaneous daily mortality estimate (M 0.62), observed during August, was similar to that reported for estuarine larval spotted seatrout *Cynoscion nebulosus* (0.64; Peebles and Tolley 1988) and, to some extent, another carangid, jack mackerel *Trachurus symmetricus* (0.80; Hewitt et al. 1985). Mortality estimates, which declined throughout September 1986 (0.35–0.18) and 1987 (0.30–0.17), were similar and were within the reported range for several larval marine species (Essig and Cole 1986, Houde 1987 and 1989, Pepin 1991). The highest daily mortality rate was associated with highest temperatures, highest macrozooplankton displacement volumes, and highest larval Atlantic bumper densities (Tables 1–3). In late September 1986, however, there was a low mortality rate during a time of relatively high Atlantic bumper densities, lower zooplankton biomass estimates, and lower temperatures. Two factors—larval size and lower water temperatures—may have influenced this lower mortality rate (Weinstein and Walters 1981). Mean larval Atlantic bumper standard lengths (1.2 mm) were similar for all the cruises. Lower surface-water temperatures, therefore, may have enhanced survival, reducing the Atlantic bumper mortality estimate. Larval growth (i.e., daily development) and mortality rates have been reported to increase with temperature (Houde 1989, Pepin 1991). The high growth-rate and mortality estimate observed in August 1986 is consistent with these findings.

The high natural mortality observed in August is probably related to predation, based on two existing theories. Larval Atlantic bumper are usually aggregated in patches (Leffler 1989) and, therefore, may offer exceptional feeding opportunities to any predator that encounters them (McGurk 1987). Pepin (1991) suggested that increased mortality rates were associated with increasing growth rates, resulting from increased encounters with predators. These higher growth rates require a higher intake of food, causing increased activity which leads to increased predator encounters.

Another possible cause for the high August mortalities may be associated with competition for limited food resources, i.e., density-dependent mortality (Cushing 1974). Food availability as indexed by the zooplankton biomass estimate was highest during August, but the high total larval fish density may have rapidly depleted the food source, causing elevated mortalities. Larval Atlantic bumper density was high during the August cruise (608.9 larvae/100 m^3) as was the total larval fish density (1838.1 larvae/100 m^3; Leffler 1989).

This study provides preliminary information on the early life history of larval Atlantic bumper. Further studies need to be conducted on larval Atlantic bumper to determine the relationship between these early-life-history parameters and fluctuating temperatures and food availability.

Acknowledgments

The authors would like to thank J. Ditty, D. Drullinger, R. Raynie, and K. Edds for assistance in the field and laboratory. Also we would like to acknowledge L. Rouse, E. Turner, C. Wilson, R. McMichael, and two anonymous reviewers for critical reviews of the manuscript, and M. Mitchell and B. McLaughlin for their assistance in preparing the graphics. Special thanks to the captains and staff at Gulf Coast Research Laboratory, Ocean Springs, MS, for use of their boats and aquarium facilities.

Financial support was provided through the Louisiana Sea Grant College Program, a part of National Sea Grant College Program maintained by NOAA U.S. Department of Commerce.

Citations

Bannister, C.A., D. Harding, and S.J. Lockwood
1974 Larval mortality and subsequent year-class strength in the plaice (*Pleuronectes platessa* L.). *In* Blaxter, J.H.S. (ed.), The early life history of fish, p. 21–37. Springer-Verlag, NY.

Boschung, H.T.
1957 The fishes of Mobile Bay and the Gulf Coast of Alabama. Ph.D. diss., Univ. Alabama, Tuscaloosa, 626 p.

Bullis, H.R. Jr., and J.S. Carpenter
1968 Latent fisheries resources of the central West Atlantic region. *In* de Witt, G. (ed.), The future of the fishing industry of the United States, p. 61–64. Univ. Wash. Publ. Fish., New Ser. 4, Seattle.

Bullis, H.R. Jr., and J.R. Thompson
1970 Bureau of commercial fisheries exploratory fishing gear research base, Pascagoula, Mississippi—July 1, 1967 to June 30, 1969. U.S. Fish Wildl. Serv., Circ. 351, 29 p.

Campana, S.E., and J.D. Neilson
1985 Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1032.

Christmas, J.Y., and R.S. Waller
1973 Estuarine vertebrates, Mississippi. *In* Christmas, J.Y. (ed.), Cooperative Gulf of Mexico estuarine inventory and study–Mississippi, p. 320–439. Gulf Coast Res. Lab., Ocean Springs.

Cushing, D.H.
1974 The possible density-dependence of larval mortality and adult mortality in fishes. *In* Blaxter, J.H. (ed.), The early life history of fish, p. 103–112. Springer-Verlag, NY.
1975 Marine ecology and fisheries. Cambridge Univ. Press, Cambridge, 278 p.

Ditty, J.G.
1986 Ichthyoplankton in nertic waters of the northern Gulf of Mexico off Louisiana: Composition, relative abundance and seasonality. Fish. Bull., U.S. 84:935–946.

Essig, R.J., and C.F. Cole
1986 Methods of estimating larval fish mortality from daily increments in otoliths. Trans. Am. Fish. Soc. 115:34–40.

Fowler, A.J.
1989 Description, interpretation and use of the microstructure of otoliths from juvenile butterfly fish (family Chaetodontidae). Mar. Biol. (Berl.) 102:167–181.

Franks, J.S.
1970 An investigation of the fish population within the inland waters of Horn Island, Mississippi, a barrier island in the northern Gulf of Mexico. Gulf Res. Rep. 3:3–104.

Gillespie, M.C.
1971 Analysis and treatment of zooplankton of estuarine waters of Louisiana. *In* Cooperative Gulf of Mexico estuarine inventory and study, Louisiana Phase IV, Biology, p. 108–175. La. Wildl. Fish. Comm., New Orleans.

Hewitt, R.P., G.H. Theilacker, and N.C.H. Lo
1985 Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser. 26:1–10.

Houde, E.D.
1987 Fish early life dynamics and recruitment variability. *In* Hoyt, R.D. (ed.), 10th annual larval fish conference, p. 17–29. Am. Fish. Soc. Symp. 2, Bethesda.
1989 Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects. Fish. Bull., U.S. 87:471–495.

Juhl, R.
1966 Experimental trawling survey along the Florida west coast. Commer. Fish. Rev. 28(6):1–5.

Klima, E.F.
1971 Distribution of some coastal pelagic fishes in the Western Atlantic. Commer. Fish. Rev. 33(6):21–34.

Lasker, R., H.M. Feder, G.H. Theilacker, and R.C. May
1970 Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345–353.

Laurence, G.C.
1978 Comparative growth, respiration, and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Mar. Biol. (Berl.) 50:1–7.
1979 Larval length-weight relations for seven species of Northwest Atlantic fishes reared in the laboratory. Fish. Bull., U.S. 76:890–895.

Laurence, G.C., A.S. Smigielski, T.A. Halavik, and B.R. Burns
1981 Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:304–311.

Leak, J.C.
1977 Distribution and abundance of carangidae (Pisces, perciformes) larvae in the eastern Gulf of Mexico, 1971–1974. M.S. thesis, Univ. Miami, Coral Gables, 83 p.

Leak, J.C., and E.D. Houde
1987 Cohort growth and survival of bay anchovy, *Anchoa mitchilli*, larvae in Biscayne Bay, Florida. Mar. Ecol. Prog. Ser. 37:109–122.

LeCren, E.D.
1951 The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca flavescens*). J. Anim. Ecol. 20(2):201–219.

Leffler, D.L.
1989 Composition, abundance, and small-scale distribution of ichthyoplankton off the Louisiana–Mississippi barrier islands, with special emphasis on the age, growth, and mortality of *Chloroscombrus chrysurus*. M.S. thesis, Louisiana State Univ., Baton Rouge, 151 p.

Lyczkowski-Shultz, J., J.P. Steen Jr., and B.H. Comyns
1988 Early life history of red drum (*Sciaenops ocellatus*) in the north central Gulf of Mexico. MASGP-88-013, Gulf Coast Res. Lab., Ocean Springs, MS, 147 p.

McGurk, M.D.
1987 Natural mortality and spatial patchiness: Reply to Gulland. Mar. Ecol. Prog. Ser. 39:201–206.

Methot, R.D. Jr., and D. Kramer
1979 Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish Bull., U.S. 77:413–423.

Parsons, G.R., and K.M. Peters
1989 Age determination in larval and juvenile sheepshead, *Archosargus probatocephalus*. Fish. Bull., U.S. 87:985–988.

Peebles, E.B., and S.G. Tolley
1988 Distribution, growth, and mortality of larval spotted seatrout, *Cynoscion nebulosus*: A comparison between two adjacent estuarine areas of southwest Florida. Bull. Mar. Sci. 42(3):397–410.

Pepin, P.
1991 Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48:503–518.

Perret, W.S., W.R. Latapie, J.F. Polland, W.R. Mock, G.B. Adkins, W.J. Gaidry, and C.J. White
1971 Fishes and invertebrates collected in trawl and seine samples in Louisiana estuaries, Section I. *In* Cooperative Gulf of Mexico estuarine inventory and study, Louisiana, Phase IV, Biology, p. 39–105. La. Wildl. Fish. Comm., New Orleans.

Power, J.H.
1989 Sink or swim: Growth dynamics and zooplankton hydromechanics. Am. Nat. 133(5):706–721.

Pritcher, C.R.
1988 Validation of a technique for reconstructing daily patterns in the recruitment of coral reef damselfish. Coral Reefs 7:105–111.

Radtke, R.L.
1984 Formation and structural composition of larval striped mullet otoliths. Trans. Am. Fish. Soc. 113:186–191.
1989 Larval fish age, growth, and body shrinkage: Information available from otoliths. Can. J. Fish. Aquat. Sci. 46: 1884–1894.

Reid, G.K.
1954 An ecological study of the Gulf of Mexico fishes in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4:1–94.

Reintjes, J.W.
1979 Coastal herrings and associated species: A profile of species or groups of species, their biology, ecology, and current exploitation with economic and social information. Prepared for Gulf of Mexico Fish. Manage. Counc. by NMFS Southeast Fish. Sci. Cent., Beaufort NC, 170 p.

Sabins, D.S.
1973 Diel studies of larval and juvenile fishes of the Caminada Pass area, Louisiana. M.S. thesis, Louisiana State Univ., Baton Rouge, 163 p.

SAS Institute Inc.
1985 SAS User's Guide: Statistics, 1982 Edition. SAS Inst. Inc., Cary NC, 584 p.

Secor, D.H., and J.M. Dean
1989 Somatic growth effects on the otolith–fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 46:113–121.

Shaw, R.F., and D.L. Drullinger
1990 Early-life-history profiles, seasonal abundance, and distribution of four species of carangid larvae off Louisiana during 1982 and 1983. NOAA Tech. Rep. NMFS 89, 37 p.

Shaw, R.F., D.L. Drullinger, K.A. Edds, and D.L. Leffler
1988 Fine-scale spatial distribution of red drum, *Sciaenops ocellatus*, larvae. Contrib. Mar. Sci. 30(suppl.):109–116.

Stuck, K.C., and H.M. Perry
1982 Ichthyoplankton community structure in Mississippi coastal waters. *In* Fishery monitoring and assessment completion report, 1 Jan. 1977 to 31 Dec. 1981, p. VI-I-1 thru VI-I-53. Proj. 2-296-R, Gulf Coast Res. Lab., Ocean Springs, MS.

Van Guelpin, L., D.F. Markle, and D.J. Duggan
1982 An evaluation of accuracy, precision, and speed of several zooplankton sampling techniques. J. Cons. Perm. Int. Explor. Mer 40:226–236.

Warlen, S.M.
1988 Age and growth of larval gulf menhaden, *Brevoortia patronus*, in the northern Gulf of Mexico. Fish. Bull., U.S. 86:77–90.

Weinstein, M.P., and M.P. Walters
1981 Growth, survival and production in young-of-year populations of *Leiostomus xanthurus* Lacepede residing in tidal creeks. Estuaries 4(3):185–197.

Williams, L.W.
1983 Larval fish assemblages of lower Mobile Bay. M.S. thesis, Univ. South. Alabama, Mobile, 55 p.

Wilson, C.A., D.W. Beckman, and J.M. Dean
1987 Calcein as a fluorescent marker of otoliths of larval and juvenile fish. Trans. Am. Fish. Soc. 116:668–670.

Yentsch, C.S., and J.F. Hebard
1957 A gauge for determining plankton volume by the mercury immersion method. J. Cons. Cons. Int. Explor. Mer 22(2):184–190.

Evaluation of ghost fishing in the Hawaiian lobster fishery

Frank A. Parrish
Thomas K. Kazama

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu Hawaii 96822-2396

Abstract.–Mortality due to retention of lobsters in derelict traps was evaluated over a 2-year period using two approaches. First, a string of eight empty, single-chamber, plastic traps was deployed at 40 m depth off Oahu, Hawaii, and monitored periodically by scuba during a 6-month period in 1990. The traps were stable and remained intact despite adverse oceanic conditions. Numerous entries and exits of lobsters were recorded. For the second test, the ability of lobsters to exit traps was tested in a series of field and laboratory trials of trap strings stocked with Hawaiian spiny lobster *Panulirus marginatus* and slipper lobster *Scyllarides squammosus*. The number of lobsters that died in stocked traps was less than 4% of the test population and differed significantly from zero only in the laboratory evaluation (χ^2 5.42, P 0.02). The two species exited similarly; however, the pattern of exits in laboratory and field tests differed significantly (χ^2 23.889, P 0.03). All lobsters exited within 56 days in a pattern generally approximating an exponential decline. Our evidence suggests that little direct mortality of lobsters is due to the inability to exit traps, and consequently ghost fishing by these traps is not considered a problem for spiny and slipper lobsters.

Manuscript accepted 14 August 1992.
Fishery Bulletin, U.S. 90:720–725 (1992).

Continued fishing by lost traps has become the focus of increasing concern by both fishery managers and scientists. The recent trend for trap fisheries to replace their degradable traps with designs made from more persistent synthetic materials has heightened the seriousness of possible ghost fishing by such unrecovered traps. Ghost fishing has been defined as the continued fishing of irretrievable gear (Smolowitz 1978). Such a definition fails to distinguish between permanent entrapment and temporary occupation of a trap (e.g., for feeding or shelter). Mortality occurring in abandoned traps should be measured to assess the impact of ghost fishing on a particular fishery.

The phenomenon of ghost fishing has been observed in a wide range of trap fisheries with diverse trap designs (e.g., High 1976, Pecci et al. 1978, Smolowitz 1978, Paul 1983). Despite this attention, few studies have effectively assessed the ghost fishing problem for any species. The more rigorous evaluations rely on continued underwater field observations of simulated lost traps (Breen 1990). With this method, mortalities have been clearly demonstrated in temperate fisheries in which animals were unable to exit traps fitted with nonreturn entrance devices. Features such as spring-loaded doors and slick plastic entrance chutes effectively reduce the ability of some animals to exit actual and simulated lost traps, resulting in reported mortalities of 26–55% (High 1976, Miller 1977, Breen 1987). Conventional wooden, two-chamber or "parlor-type" traps designed for the American lobster *Homarus americanus* have produced mortalities of 12–25% (Sheldon and Dow 1975, Pecci et al. 1978, Smolowitz 1978).

Ghost fishing poses a potential risk to at least some trap fisheries, and such a risk requires assessment for each species and trap configuration. Tropical lobsters have been largely neglected in the controlled evaluation of mortality by ghost traps. Isolated anecdotal reports of tropical lobsters found in lost traps (Sutherland et al. 1983) and tank studies made to date (Paul 1983) do little to predict realistic, long-term effects of lobsters interacting with modern traps in the field.

Hawaii's lobster fishery targets two species, Hawaiian spiny lobster *Panulirus marginatus* and slipper lobster *Scyllarides squammosus*. A laboratory study by Paul (1983) used California parlor-type traps made of wire to determine the effectiveness of escape vents in releasing undersized Hawaiian spiny lobster. Paul (1983) suggested that ghost fishing might occur in these traps and recommended that the Hawaiian fishery consider incorporating degradable escape panels to facilitate the escape of adult lobsters. By 1985 the fishery had adopted a more cost-effective molded-plastic trap design as the standard gear. Degradable panels have not been included.

In 1989 the Hawaiian lobster industry reported that more than 1 million traps were set in the Northwestern

Hawaiian Islands (NWHI); an estimated 2000 of these traps were unrecovered (Landgraf et al. 1989). The annual accumulation of lost plastic traps on the banks where commercial trapping occurs must be considered a potential hazard to the lobster stocks. No field studies have been done on the interactions between lost traps and the adults of the two target lobster species. The objectives of this study were to (1) evaluate the persistence of lost commercial traps under field conditions, (2) estimate retention of target species in plastic traps with bait depleted, and (3) assess mortality of lobsters unable to exit traps.

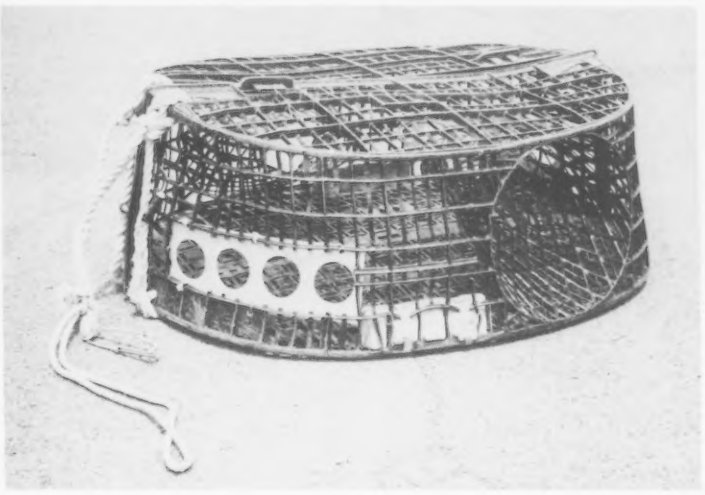


Figure 1
Plastic trap used in the Hawaiian commercial lobster fishery.

Methods

Study sites

The prohibitive cost of prolonged, ship-supported diving operations in the NWHI dictated that all field experiments be conducted at Oahu. Sites close to the windward shore of Oahu provided appropriate depths (30–40 m) and habitat consistent with the NWHI commercial banks. The area is known to harbor exploitable numbers of the lobster fishery's target species. Its heavy seas, strong bottom surge, and swift currents (Bathen 1978) might mimic NWHI conditions and thus could test the stability of lost traps. Traps placed in such rough conditions, without surface markers, were unlikely to be disturbed by fishermen and other recreational users.

Trap stability and faunal interactions

A string of eight empty traps was deployed in a linear orientation from February to July 1990. The selected area afforded two types of adjacent habitat—high-relief rugose bottom, and hard relatively-flat bottom—allowing comparisons of trap stability and use by lobsters in the different environments. Individual traps were set 10 m apart, four on high-relief bottom and four on adjacent even bottom. The molded-plastic traps (Fig. 1) used in the study were a standard commercial model employed throughout the commercial fishery in Hawaii (Fathoms Plus Marine Implementation, P.O. Box 6307, San Diego, CA 92106). Each trap consisted of a single chamber with two side entrances and was weighted with about 10 kg of lead, as is conventional in the fishery. Traps remained in place over a 6-month period. They were observed monthly by scuba divers during three dives conducted at 48-hour intervals. Physical condition, movement, and contents of the traps were noted on each dive, along with general observations of the surrounding area. The monthly censuses recorded the initial presence of lobsters from the surrounding study site and any exits or entries over the following 4 days. The area in and under the traps was examined for exoskeleton remnants that might indicate molting or mortality. One additional trap with its hinge pins removed was deployed on flat bottom near the trap string to mimic a trap with corrodible hinge pins that had deteriorated.

Trap stocking experiment

In the summers of 1990 and 1991, traps of the same type (Fig. 1) were deployed in the field and laboratory, and stocked with spiny and slipper lobsters from the NWHI to evaluate their ability to exit and the extent of mortality. Prior to the traps being stocked, lobsters had spent 3–8 days in transit in continuously-flushing shaded bait wells where they were fed daily. Mean carapace lengths were 87.6 mm (N 96, range 67.4–121.7 mm) for spiny lobster, and 83.3 mm (N 96, range 50.1–99.7 mm) for slipper lobster. Antennae were tagged with color-coded, plastic, self-locking, electrical ties to permit visual identification of individuals without their being handled during the experiment. Molt stage

of lobsters prior to their deployment in traps was determined using Lyle's (1982) adaptation of Drach's (1939) staging technique.

In the field test, 128 tagged lobsters were placed by divers in 4 strings of 8 unbaited traps each (2 spiny and 2 slipper lobsters per trap). Two strings were placed on and around high-relief substrate, one in summer 1990 and the other in summer 1991; two strings were placed on relatively-flat hardbottom, at least 300 m from any relief that could provide lobsters shelter, in summer 1991. The contents of the traps were checked every 48 hours until all tagged lobsters had exited or died.

In the laboratory trials, 64 additional tagged lobsters were placed in 16 traps (2 spiny and 2 slipper lobsters per trap) in a large, shaded, outdoor concrete tank. Throughout the tank, food and other suitable shelter were provided outside the traps to encourage exiting. Contents of the traps were monitored daily, and any lobsters found outside the trap in which they were originally stocked were removed from the tank. Lobster death totals in the laboratory (where predation could not occur) and in the field were compared in an attempt to separate losses by predation from other mortality (e.g., starvation, conspecific aggression) in the field.

This study employed a modified experimental cohort design to examine the effects of multiple categories (replicate, habitat type, species) on exiting by lobsters. The design permits cross-classified categorical analysis to be applied (Fienberg 1987). Using chi-square tests, comparisons were made between replicates, habitat types, and species in a systematic order. Categories were collapsed or pooled when justified by the lack of significant differences (Siegel and Castellan 1988).

Results

Trap stability and faunal interactions

Estimated seas of 4–6 ft and currents of 1–2 knots were common at the study site. They produced no observable effect on the physical integrity of the plastic traps. Movement of traps across the substrate was not detected, despite frequent observations of the interconnecting groundline actively moving in the bottom surge. The two halves of the trap without hinge pins shifted 2 cm apart. Over the 6-month period, the traps became encrusted with sessile organisms, including bryozoans, corals, and fish eggs. Occasionally adult fish larger than the opening of the escape vent were found in the traps; however, most of these departed through the trap entrance as a diver approached.

Adults of both spiny and slipper lobsters local to the surrounding study site entered the traps. Of the 12 such occurrences of lobsters recorded during the 6-month survey, 7 lobsters left before the last inspection of the monthly observation period, indicating that they did not occupy the traps for more than 30 consecutive days. Three lobsters were observed entering and exiting within the same 48-hour observation period. Nine of the 12 lobsters were found in traps on even bottom.

One dead spiny lobster comprised the only mortality observed within the 6-month field evaluation. Postmortem examination and the presence of lobster debris in the area around the trap suggested death by predation. Sightings of known predators such as octopus, eels, jacks, and sharks were routine. Large eels often occupied the traps, occasionally with lobsters.

Trap stocking experiment

Molt-stage evaluation indicated that 27% of the spiny lobsters and 1% of the slipper lobsters were in the premolt stage at deployment. Mortality was limited to seven spiny lobsters, five in the laboratory and two in the field. All of these lobsters were in premolt stage at deployment and died during or shortly after molting. Despite the limited mortality, the number of deaths in the laboratory trials differed significantly from zero

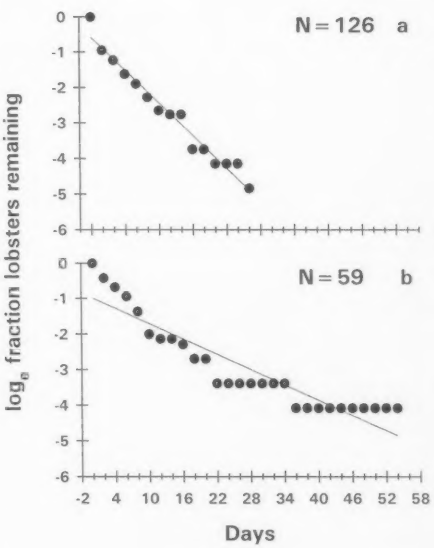


Figure 2
Persistence of occupancy of plastic traps stocked with spiny *Panulirus marginatus*, and slipper *Syllarides squamosus*, lobsters (combined) in the (a) field and (b) laboratory.

(χ^2 5.42, P 0.02). This was not true for the field trials (χ^2 2.06, P 0.15), and mortalities in the laboratory and field were significantly different (χ^2 4.74, P 0.03). Consequently, the two test situations were evaluated separately, with all animals that died excluded from the trap-occupation analysis.

Contingency tables were used to test for differences in the exit distributions for various groups of the data (Fienberg 1987). Within each species, the distributions of exits were first compared between replicate trap strings within the same habitat type and were found not to be significantly different (spiny lobster—high relief, χ^2 3.22, P 0.50; even substrate, χ^2 10.00, P 0.19; slipper lobster—high relief, χ^2 3.33, P 0.50; even substrate χ^2 9.52, P 0.22). Therefore, the distributions of exits for the two replicates were pooled within each habitat type. Within each species, exits were then compared for the effect of the two habitat types and were found not significantly different (spiny lobster—χ^2 10.81, P 0.21; slipper lobster—χ^2 4.53, P 0.72). The distributions of two habitat types were then pooled within each species, and exits of the two species were not significantly different (χ^2 16.93, P 0.08). Consequently, the distributions of the two species in all field trials were combined (N 126 lobsters after 2 early mortalities) for further comparisons.

Within each species, exits observed in the tank were compared with the field data pooled by replicate and habitat type and were not significantly different (spiny lobster—χ^2 14.42, P 0.21; slipper lobster—χ^2 13.63, P 0.09). Exits of spiny and slipper lobsters in the tank were not significantly different (χ^2 11.55, P 0.32), and the data were subsequently pooled (N 59 lobsters after 5 early mortalities). A comparison of exits of all lobsters in the tank (pooled) and all lobsters in the field (pooled) showed a significant difference (χ^2 23.889, P 0.03).

Half of the 126 spiny and slipper lobsters stocked in the field and 33% of the lobsters stocked in the laboratory exited within 48 hours after being placed in the traps. Ninety percent or more of the exits in both tank and field trials occurred within the first 16 days. All field animals had left by day 30, and all laboratory animals by day 56. The overall exit pattern of the lobsters suggested an exponential model. The data were fitted to the log-transformed exponential function

$$\ln_e (N_t/N_0) = bt,$$

where N_t is the number of lobsters remaining after time t from N_0 lobsters initially stocked. The parameter b was estimated with a log-linear regression procedure for the field traps ($b = -0.16$/day; r^2 0.992, SE 0.284, $P<0.001$) and for the laboratory traps ($b = -0.094$/day, r^2 0.961, SE 0.632, $P<0.001$; Fig. 2).

Stocked spiny and slipper lobsters exited and reentered field traps in at least 13 instances; 6 lobsters returned to the same trap. One spiny lobster was observed exiting three traps within 6 days.

Discussion

Trap stability

The lack of structural damage and appreciable movement of the plastic traps in the field contrasts with the popular opinion of experienced fishermen that lost traps break up and roll off the banks into waters beyond the depth range of lobsters. Fishermen routinely report movement of trap strings as a result of powerful swells moving across the commercial banks. Despite the frequently observed movement of the groundline by swells at the Oahu study site, it is likely that the study site does not fully duplicate the power of the long-term swells common in the NWHI. Lost traps may not shift on the bottom as much as actively fished traps. Buoys and interconnecting polypropylene line provide additional lift and resistance to water motion; therefore, fully rigged strings of traps are more likely to move than isolated traps severed from the groundline. A 1990 systematic diving survey of 33 sites around 2 of the prominent NWHI commercial lobster fishing banks revealed only 2 mangled derelict traps (F. Parrish, unpubl. data). The failure to locate large amounts of lost gear may be partly explained by this survey being incidental to other work. Total gear losses in 1989 averaged about 1 trap/nm^2 over the total estimated area of the lobster fishing grounds (Landgraf et al. 1989). Lost gear could be heavily concentrated in a few of the more intensively fished areas that the survey may have missed.

A trap manufacturer (Fathoms Plus Marine Implementation) has made available a corrodible pin which is intended to allow the halves of plastic traps to eventually fall apart once the pin deteriorates. The fact that our pinless trap remained relatively intact for 6 months in the field suggests that the synthetic plastic clips on the trap roof will continue to hold the trap together, especially for fisheries conducted in calmer seas.

Mortality and movement of lobsters

Seven deaths among the 192 spiny and slipper lobsters within the 56-day study represent low mortality when compared with the natural mortality estimates from the fishery population modeling by Haight and Polovina (1992). Extrapolation of the experiment's percentage of mortality from 2 months to 1 year (22%) is close to half the fishery's annual estimated natural mortality (40%). The fact that only animals that began the trials

in premolt condition died suggests that lobsters at this stage are less fit. The probability that this mortality would occur only with premolt individuals by chance alone is <0.001 (Agresti 1990). Increased vulnerability to a poor physical environment, conspecific aggression, or predation have been associated with molting (Conan 1985). It seems likely that the higher percentage of spiny lobster in premolt stage accounts for some of the difference in mortality between spiny and slipper lobsters.

The significantly higher mortality observed in the laboratory compared with the field does not support the idea that undetected predation substantially affected the field results. The relatively low absolute level of total mortality suggests that such predation is probably minimal at the field site. However, with mortality being higher in the laboratory than in the field, no estimate of predation is possible.

More than twice as many deaths were observed in the laboratory as in the field, even though the field trials involved twice as many lobsters and three times as many were in the premolt stage. This suggests a less healthy or fit laboratory population, which is consistent with the significantly slower exit of pooled species from traps in the laboratory versus in the field. Aspects of the laboratory environment (e.g., water quality, lighting, diet) may have degraded the physical condition of the lobsters or affected their behavior, inhibiting their exit, or providing less inducement to leave the traps than that encountered in the field. It seems likely that our field assessment provides a better estimate of natural exit patterns.

With a study design similar to ours, Munro (1974) examined the rate of fish exiting unbaited traps. His theoretical model suggests that the number exiting per day may be a fixed fraction of the current trap occupancy, and that catch eventually reaches an asymptote when trap entrances are balanced by exits. Our number of stocked lobsters declined approximately exponentially, approaching zero asymptotically. However, the total occupancy of traps declined daily until it reached a low and varying level at which exits were roughly matched by entrances of lobsters. This final, low level of trap occupancy at the end of the stocking experiment seems consistent with native occupancy observed during the monthly field monitoring.

In our stocking tests, some individuals likely left a trap and reentered it undetected between censuses, particularly in the field test where the observation interval was 48 hours. Based on independent probabilities of exit and entry estimated from our field data, the theoretical joint probability of such reentry was as high as 0.06, and probably about 12 individuals left and reentered the same trap undetected during the full 26-day field stocking experiment.

Conclusion

Our results indicate that spiny and slipper lobsters are not restrained by lost molded-plastic traps for periods long enough to cause serious harm. There is no evidence that such lost traps result in increased mortality. The absence of any apparent trap-induced mortality and the low incidence of identifiable in-trap mortality due to predation suggest that ghost fishing by these traps contributes little to the total mortality of the population. Such traps, when unbaited and intact, may best be considered short-term artificial shelters that lobsters enter and exit occasionally, more or less at will.

Acknowledgments

Thanks are due to Steve Kaiser for advice on selection of study sites and to Bill and Joanne Goebert for providing ready access to those sites. Ray Boland, Karl Bromwell, Theresa Martinelli, and Leslie Timme assisted in the rigorous program of field monitoring. Greatly appreciated are the statistical and substantive comments of Deborah Goebert, Robert Moffitt, James Parrish, and Jeffrey Polovina.

Citations

Agresti, A.
1990 Categorical data analysis. John Wiley, NY, 558 p.

Bathen, K.H.
1978 Circulation atlas for Oahu, Hawaii. Misc. Rep. UNIHI-SEAGRANT-MR-78-05, Univ. Hawaii Sea Grant Coll. Prog., Honolulu, 22 p.

Breen, P.A.
1987 Mortality of Dungeness crabs caused by lost traps in the Fraser River estuary, British Columbia. N. Am. J. Fish. Manage. 7:429–435.
1990 A review of ghostfishing by trap and gill nets. *In* Shomura, R.S., and M.L. Godfrey (eds.), Proceedings, Second international conference on marine debris, 2–7 April 1989, Honolulu, p. 571–599. NOAA Tech. Memo. NMFS-SWFSC-154, NMFS Southwest Fish. Sci. Cent., Honolulu.

Conan, G.Y.
1985 The periodicity and phasing of molting. *In* Wenner, A.M. (ed.), Crustacean issues, factors in adult growth, vol. 3, p. 73–99. A.A. Balkema, Boston.

Drach, P.
1939 Mue et d'intermue chez les Crustaces Decapodes. Ann. Inst. Oceanogr. 19:103–392.

Fienberg S.E.
1987 The analysis of cross-classified categorical data, 2d ed. MIT Press, Boston, 198 p.

Haight W.R., and J.J. Polovina
1992 Status of lobster stocks in the Northwestern Hawaiian Islands, 1991. Admin. Rep. H-92-02, NMFS Southwest Fish. Sci. Cent., Honolulu, 19 p.

High, W.L.
1976 Escape of Dungeness crabs from pots. Mar. Fish. Rev. 38(4):19–23.

Landgraf, K.C., S.G. Pooley, and R.P. Clarke
1989 Annual report of the 1989 western Pacific lobster fishery. Admin. Rep. H-90-06, NMFS Southwest Fish. Sci. Cent., 30 p.

Lyle, W.G.
1982 Molt stage determination in the Hawaiian spiny lobster *Panulirus marginatus*. M.S. thesis, Univ. Hawaii, Honolulu, 29 p.

Miller, R.J.
1977 Resource underutilization in a spider crab industry. Fisheries (Bethesda) 2(3):9–13.

Munro, J.L.
1974 The mode of operation of Antillean fish traps and the relationships between ingress, escapement, catch and soak. J. Cons. Cons. Int. Explor. Mer 35:337–350.

Paul, L.M.B.
1983 Investigations into escape vent effectiveness and ghost fishing in captive populations of the spiny lobster *Panulirus marginatus*. *In* Grigg, R.W., and K.Y. Tanoue (eds.), Proceedings, Second symposium on resource investigations in the Northwestern Hawaiian Islands, vol. 2, p. 283–295. Misc. Rep. UNIHI-SEAGRANT-MR-84-01, Univ. Hawaii Sea Grant Coll. Prog., Honolulu.

Pecci, K.J., R.A. Cooper, C.D. Newell, R.A. Clifford, and R.J. Smolowitz
1978 Ghost fishing of vented and unvented lobster, *Homarus americanus*, traps. Mar. Fish. Rev. 40(5-6):9–24.

Sheldon, W.W., and R.L. Dow
1975 Trap contributions to losses in the American lobster fishery. Fish. Bull., U.S. 73:449–451.

Siegel, S., and N.J. Castellan
1988 Nonparametric statistics, 2d ed. McGraw-Hill, NY, 399 p.

Smolowitz, R.J.
1978 Trap design and ghost fishing: An overview. Mar. Fish. Rev. 40(5–6):2–8.

Sutherland, D.L., G.L. Beardsley, and R.S. Jones
1983 Results of a survey of the south Florida fish-trap fishing grounds using a manned submersible. Northeast Gulf Sci. 6(2):279–183.

Movements of acoustically-tagged yellowtail rockfish *Sebastes flavidus* on Heceta Bank, Oregon

William G. Pearcy
College of Oceanography, Oregon State University, Corvallis, Oregon 97331-5503

Abstract. – Movements of 25 yellowtail rockfish *Sebastes flavidus* on Heceta Bank, off Oregon, were studied by acoustical tagging and tracking during the summers of 1988–90. Some fish were tracked discontinuously up to 1 month after transmitters were inserted into their stomachs. In each year, some fish remained at the capture site after release or returned after displacement to a different release site. In 1990, the year of most intensive tagging, 11 of 12 fish were detected near the capture location 13 days after release in August 1990, including 3 of 4 fish displaced 0.5 nmi (0.9 km), all 4 fish displaced 2.0 nmi (3.7 km), and all 4 of the fish released at the capture site. One fish homed overnight from the release site 0.5 nmi away. In September 1990, 1 month after release, eight of these fish had dispersed up to 0.1–0.7 nmi (0.2–1.3 km) to the south of their capture location, suggesting a change in site fidelity. Pressure-sensitive transmitters showed that tagged yellowtail rockfish usually remained at midwater depths of 25–35 m, well above the sea floor depth of ~75 m. Rapid descents to nearbottom depths were common, but no obvious diel vertical or horizontal migrations were detected.

Manuscript accepted 13 July 1992.
Fishery Bulletin, U.S. 90:726–735 (1992).

The yellowtail rockfish *Sebastes flavidus* is a common rockfish along the west coast of North America. It is caught by both commercial and recreational fishermen and was one of the most abundant rockfish species in commercial groundfish landings from the U.S. west coast from 1982 to 1990 (Pacific Fisheries Management Council 1991).

Schools of yellowtail rockfish may persist at the same location for many years. Carlson (1986) reported that a school of adult yellowtail rockfish in southeastern Alaska consisted of individuals from one or two year-classes and had negligible recruitment over an 11-year period. Because their aggregrations may be site-specific with limited interchange of adults, and because rockfish are long-lived, late-maturing, and of low fecundity (Gunderson et al 1980, Love et al. 1990, Eldridge et al. 1991), overfishing or disturbances, such as habitat modifications from offshore mining or petroleum development, may have long-lasting effects in a local area. On the other hand, a rockfish species whose individuals move freely from reef to reef may be less vulnerable to localized disturbances (Love 1979). The stability and areal range of rockfish aggregations have important implications for assessment, availability, and management of rockfish species.

The yellowtail rockfish is the most abundant, large-sized schooling fish seen from submersibles over the shallow, rocky areas on the top of Heceta Bank, a deep reef located ~55 km off the central Oregon coast (Pearcy et al. 1989; Figs. 1 and 2). Large pelagic schools, sometimes of a thousand or more individuals, were observed over shallow portions of the bank (<150 m) during the summer. Based on both observations from submersible dives and the occurrence of large echo-groups recorded by the ships' echosounders, these schools were often associated with pinnacles or high-relief topography (Pearcy et al. 1989).

During one dive, a school of yellowtail rockfish followed the submersible along the bottom for over an hour before abruptly turning and swimming back toward the location where the school was initially encountered (Pearcy et al. 1989). This observation and those of Carlson and Haight (1972), who found that individual rockfish returned to a home site in southeast Alaska after being displaced as far as 22.5 km, suggest that schools of yellowtail rockfish may have home ranges centered around a specific site on the bank.

Pelagic rockfishes, such as the yellowtail rockfish, may range over wider areas than benthic rockfishes. However, little is known about the vertical distribution or diel vertical migrations of yellowtail rockfish, or the relationships between vertical and horizontal movements.

This study used acoustical tracking to determine the horizontal and vertical movements and site-specificity of yellowtail rockfish on Heceta Bank. In this paper, I define site-specificity as the tendency of fish to inhabit a specific localized area as opposed to free-ranging or vagrant

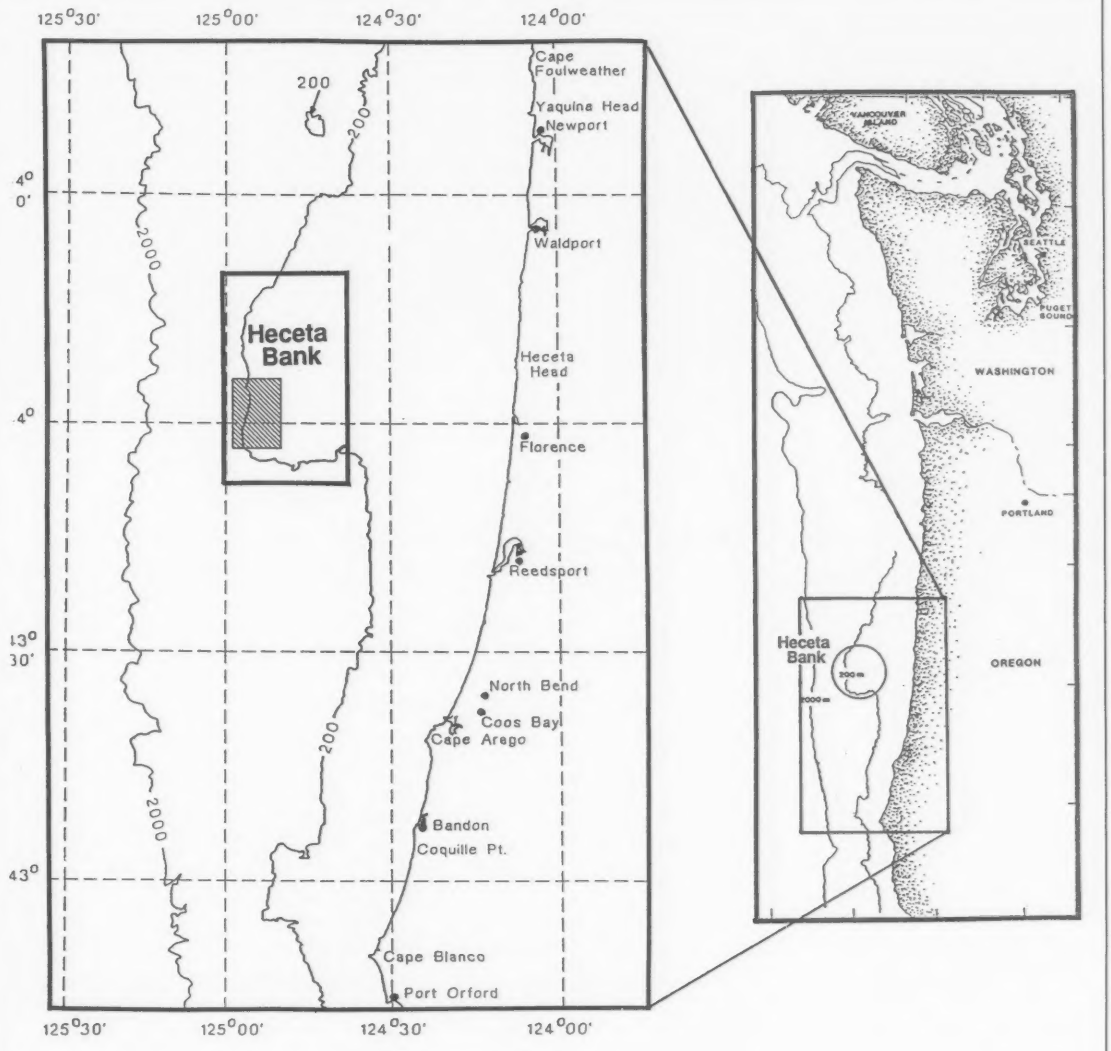


Figure 1

Location of Heceta Bank off Oregon. Hatched area of the bank encompasses the area of this study as shown in Figure 2 (depth contours in meters).

behavior. Homing is defined as returning to a site formerly occupied instead of to equally probable locations. Homing does not imply a direct, straight-line course back to the home site.

Yellowtail rockfish are ideal for acoustical tracking because they are common, large in size, and do not suffer from the lethal embolisms of other rockfishes when brought to the surface, but instead expel swimbladder gases during decompression*.

* Bubbles of gas were observed emanating from the region of the opercle as yellowtail rockfish were reeled from about 2–3 m depth to the surface. By immersing fish in tanks aboard ship, these bubbles were seen forming and being expelled from under the thin skin between the last gill and the cleithrum anterior to the base of the pectoral fin. Samples of the gas were collected in syringes and analyzed with a microgasometer using the methods of Scholander et al. (1955). The gas was comprised of about 75% oxygen, indicating that gases from the swimbladder were released without causing lethal embolisms when yellowtail rockfish were rapidly decompressed.

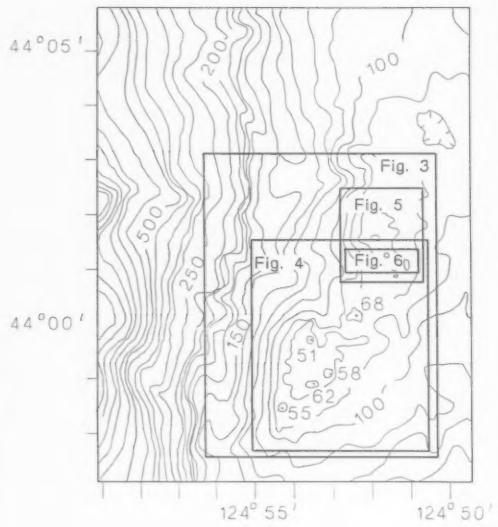


Figure 2
Topography of the southern portion of Heceta Bank and the areas encompassed in Figures 3–6. Depths are in meters.

Table 1
Information on tag retention in 5 yellowtail *Sebastes flavidus*, and 5 black *S. melanops*, rockfishes aboard ship (S) and in the laboratory ashore (L). ARM = tags with hooks (anti-regurgitation mechanisms).

Date	S/L	Tag	Days to regurgitate (or die)
S. flavidus			
Sep 1988	S	External	(3)
	S	Stomach	1,2,(6)
Aug 1990	L	Stomach–ARM	11
S. melanops			
Apr 1990	L	Stomach	1
	L	Stomach–ARM	9
Jul 1990	L	Stomach	0.5
	L	Stomach–ARM	2,89

Methods

Yellowtail rockfish were captured with hook-and-line during the daytime and placed in deck tanks with circulating seawater. Acoustical transmitters were inserted into the stomachs of large (42–54 cm fork length), active, uninjured, unanesthetized fish with a 1 cm diameter rod. Most fish were males. Fish were released within 15 min at the capture site or within 30 min at displaced locations. Displaced fish were released over bottom topography and depths known to be inhabited by yellowtail rockfish (except in 1988), and within 2 nmi of the capture location to facilitate survey of several release sites during a cruise. They were tracked using a directional hydrophone and acoustical receiver. Four fish tracked during 1989 were also tagged with external Floy tags.

Preliminary tagging

Before this study began, a few tests were conducted in circulating seawater tanks aboard ship or in the laboratory to evaluate methods of tagging pelagic rockfishes on five yellowtail and five black rockfishes (Table 1). Dummy tags of the same dimensions and weight as those used in the study were inserted into the stomach or attached externally to the side of fish under the dorsal fin. The external tag attachment, similar to the one used by Matthews et al. (1990) for benthic rockfish, caused one fish to list to one side and interfered with its swimming. It died after 3 days in the ship's tank. Three fish with tags inserted in their stomachs had normal orientation in deck tanks and were more active. One of these fish died after 6 days.

Stomach insertion of tags was used in this study. This method is quick and minimizes handling and trauma to the fish (Stasko and Pinock 1977). The major disadvantage was possible regurgitation of tags (Table 1 and Results), although Stasko and Pincock (1977) reported that transmitters inserted into the stomachs of many other species of fishes were not disgorged. During the last year, to increase the retention of tags in the stomachs, one or two small (no. 18 steel dry fly) hooks were attached to the ends of tags with epoxy as anti-regurgitation mechanisms (ARM's). Hooks protruded 2 mm from the tag. In experiments in large aquaria or tanks in the laboratory, tags with ARM's stayed inside either black rockfish *S. melanops* or yellowtail rockfish a total of 2, 9, 11, and 89 days compared with 0.5, 1, 1, and 2 days (and one that died after 6 days) for controls without ARM's (Table 1).

Equipment

Acoustical tracking equipment (VEMCO Ltd.) was used in this study, including a VR-60 receiver with preset channel frequencies, a telemetry decoder and display unit, directional hydrophone, and transmitters or tags with five different crystal-controlled frequencies. Transmitters were 16 mm in diameter, 48–65 mm in length, with batteries of 4.5, 9, 21, and 60 days rated life-span. In 1990, transmitters with the same frequencies had different pulse widths and pulse periods which

were decoded and displayed by the receiver. The transmitters had a rated range of 500–1500 m.

Pressure-telemetering transmitters with battery durations of 4.5 days were used in 1989 and 1990. The pulse rates of these transmitters were linearly proportional to pressure, and individual calibrations were incorporated into the receiver program. The manufacturer claimed accuracy was 5% of the full range, or 5 psi (~3 m depth), similar to my test of two tags lowered vertically on a metered line at sea. Data on depths of fish and time of day from these transmitters were printed at regular intervals aboard ship and stored in the receiver. During 1989, depths and times were recorded manually every 5 min or less. During 1990, data on time and depth were stored automatically by the receiver every 0.5 sec. Median depths were calculated for every 25-sec period and plotted by computer.

Field procedures

Research was conducted using either the RV *William A. McGaw*, a 32 m ship used to support submersible research, or the FV *Corsair*, an 18 m trawler. Echosounders were used to scout concentrations of fish over the shallow (60–90 m) portions of Heceta Bank. When dense midwater schools of fish were detected, weighted fishing lines with jigs were lowered to catch fish. Only yellowtail rockfish were caught from these midwater schools, which were usually at depths of 20–40 m. Often the schools were so compact that our fishing weights bounced off fish at these depths. If yellowtail rockfish were readily caught, our position was recorded and an anchored surface float was released from the *Corsair* to provide a fixed reference to prevent drifting off-station and assist tracking of fish.

Transmitter signals were detected with a directional hydrophone attached to the end of a 4 m rotatable pole mounted to the side of the vessels. The hydrophone pole was rotated through 360° until the signal strength of a transmitter was maximal. Then the vessel headed directly toward the transmitter. Signal strength increased as the range closed. When signal strength was equally high in all directions or when the direction of the signal decreased rapidly, we assumed that the fish was in the vessel's immediate vicinity and our location was then determined by LORAN C. Repeated positions for stationary transmitters on the bottom were within 0.1 nmi (~180 m) from one another. Repeatable accuracy of Loran C for one vessel is about 100 m (Dugan and Panshin 1979).

Results

Horizontal movements

1988 (Fig. 3) Four yellowtail rockfish were caught near the bottom, tagged, and released during September 1988. Three fish were released where they were caught, and the fourth was displaced about 1 nmi seaward of its catch location. Fish 1 was caught and released over a shallow (71 m), high-relief rocky area of Heceta Bank on 15 September (Fig. 3). Three locations were determined

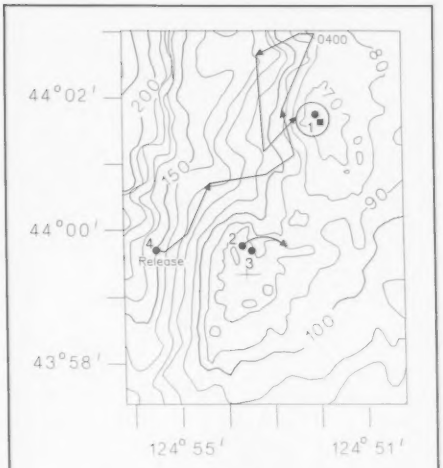


Figure 3
Locations and tracks of yellowtail rockfish *Sebastes flavidus* tagged and released in 1988. Fish 1, released 15 September at 1919 h (●), was located 24 h later (■), and was found within the open circle (O) during seven intervening fixes. Fishes 2, 3, and 4 were released 13 September (●) and followed indicated paths. Fish 3 moved less than 200 m.

immediately after release, three after 12 h, and two after ~24 h. All locations were within 0.5 nmi of one another, and the last was 0.1 nmi from the capture site. Fish 2 and 3 were caught, released, and detected once over the southernmost shallow portion of Heceta Bank at a depth of 80 m on 13 September. One of these fish was located ~0.75 nmi (1400 m) east of its capture location after 7 h. The other fish was found within 200 m of the release site 17 h after release.

To determine if a stationary transmitter location was the result of a regurgitated tag, the submersible *Delta*, with a separate hydrophone and receiver, dove on Fish 3, which remained close to the release site. The ship maintained position over this transmitter as the submersible was launched. Although a strong signal was recorded from the transmitter, its bearing changed frequently, indicating that the tag was moving and had not been regurgitated. This was confirmed when the bearing of the transmitter changed 180° as a school of several hundred fish swam under the submersible. The fish transmitting the signal had two external Floy tags but was not seen.

The fourth fish was captured at the southern high spot of Heceta Bank (80 m depth, same date and capture site as Fishes 2 and 3) and released 27 min after capture 1.3 nmi offshore in a habitat where yellowtail rockfish were rarely seen—where the bottom was 150 m, flat, and comprised of fine sediments. Between 1727 h on 7 September and 0730 h the next day, this fish was tracked continuously (Fig. 3). It moved to the northeast until 0400 h, turned south, but then resumed its northeasterly course, ending up near the 75 m depth contour just west of a shallow region of the bank, about 2 nmi from its capture location.

1989 (Fig. 4) Two experiments were conducted in 1989 to further investigate horizontal movements: one involved three fish caught and released with pressure-telemetering transmitters at a station on 21 August (1 fish) and 24 August 24 (2 fish). The other experiment included six fish, three of which were released at the capture site and three displaced 1.1 miles away, on 25 August. All fish were caught in midwater at ~79 m.

Fish 2 in the first experiment was released at site A and was tracked continuously for 11 h after release. During this time it stayed within ~0.2 nmi of the release site, which was marked by a surface buoy. We returned to this location 36 h later and found this fish 0.5 nmi to the east. After 1.5 h it returned to the release site and was located several times in this vicinity during the next 56 h (Fig. 4).

Two other fish were caught, tagged, and released 3 days later, at site B, and tracked for about 24 h. Acoustical signals of these two fish stayed within 0.2 nmi of the release location during this period.

In the second experiment, six fish were caught at site B on 25 August. Three fish (10, 11, 12) were released at the capture location and three (7, 8, 9) were displaced 1.1 nmi to the northeast of site C and released in 77 m of water. When we returned to these locations 9 days later, two (7 and 9) of the three tags from fish displaced to site C were detected and remained there over the next 36 h. Distinctive double pings from these two tags were heard on the receiver, indicating that the tags had been regurgitated and were on the bottom.

Fish 10 and 11, which were released at capture site B, were detected ~0.1 nmi south of site B 9 days after capture. Signals from the third fish (12) were not detected. The transmitter from displaced Fish 8 was detected ~0.4 nmi to the east of the capture site. Within the next 36 h, this fish moved to within 0.2 nmi of the capture location, and its last position was 0.3 nmi from the capture site.

The submersible *Delta* was used to dive on one of the tags that was stationary at the displacment location (site C). This transmitter was found lying on top of a large rock.

1990 (Figs. 5 and 6) During 1990, transmitters with ARM's were inserted into 12 yellowtail rockfish. All fish were caught during early evening (1900 h) on 15 August in mid-

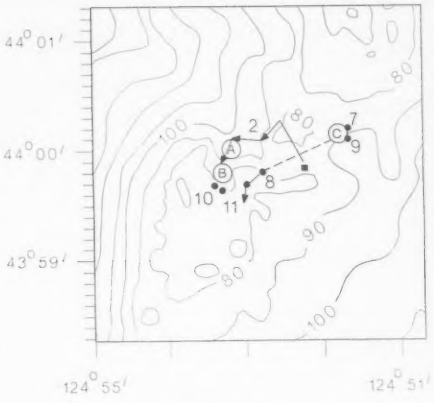


Figure 4
Locations and tracks of yellowtail rockfish *Sebastes flavidus* released in 1989. See text for details. Dashed line is the assumed path of Fish 8.

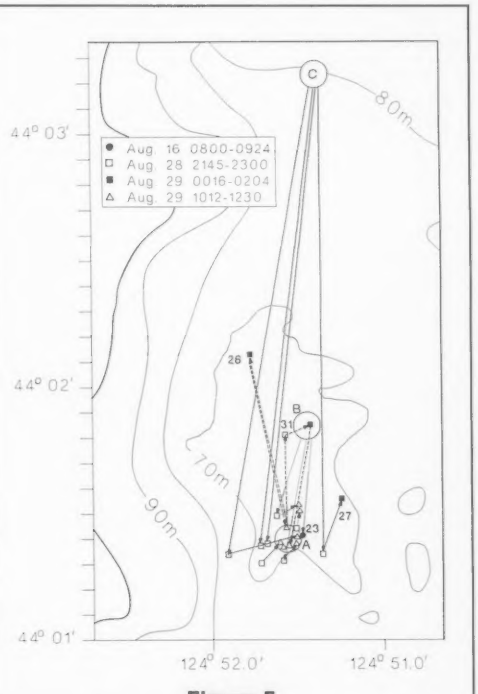


Figure 5
Tracks of 11 yellowtail rockfish *Sebastes flavidus* captured at site A and released at sites A (dashed lines), B (dotted lines), and C (solid lines) on 15 August 1990. Symbols designate dates and times that positions were obtained (see legend).

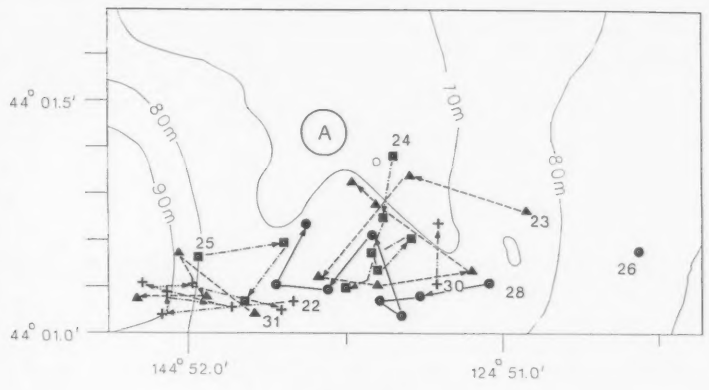


Figure 6

Tracks of eight of the yellowtail rockfish *Sebastes flavidus* released on 15 August, one month later during the period 16–18 September 1990. Symbols designate positions of each fish.

water above a 68 m rocky bottom. Four of these fish were released at capture site A, four at 0.5 nmi to the north (site B, bottom depth 70 m), and four at 2.0 nmi to the north (site C, bottom depth 87 m) (Fig. 5). The two release sites to the north of the capture site had high-relief bottom topography, similar to the capture site. In addition, schools of rockfish, similar in appearance acoustically to those comprised of yellowtail rockfish, were observed in the vicinity of the two displacement sites. Since yellowtail rockfish are numerous over shallow (<100 m) rocky ridge, boulder, and cobble habitats of Heceta Bank, and schools of yellowtail rockfish were seen from submersibles near release sites B and C (Pearcy et al. 1989, Hixon et al. 1991), I assumed that the transplant release sites were habitable by yellowtail rockfish.

The morning after the releases, all four of the transmitters in fish released at capture site A were detected within 0.1 nmi of site A. One of the fish (23) released 0.5 nmi to the north returned to the capture site overnight, after 17 h. No transmitters were detected at the other two release sites on the following day when the ship passed over these locations and departed the bank.

Eleven of the twelve fish were located 13 days after release when we returned to Heceta Bank, including all four released at site C (2.0 nmi to the north) (Fig. 5). The missing transmitter was from site B. All 11 fish were found at least once within 0.15 nmi of the capture site (Fig. 5). These results are evidence for a strong homing tendency.

Two fish that were caught and released at the original capture location (site A) showed the most extensive short-term movements (Fig. 5). Fish 26 was located 0.8 nmi and Fish 31 was found 0.5 nmi north of site A during the night and early morning of 28–29 August, 14 days after release. Both returned to site A about 11 h later. Fish 27, displaced to site C, was found 0.15 nmi east of capture site A and then moved 0.24 nmi to the north during a 2-hour period on the evening of 29 August.

One month after releases, we returned to the capture location to study longer-term movements. No transmitters were detected in the immediate vicinity of the original capture location. Using an expanding rectangular search pattern, 8 of the 12 transmitters were discovered, all south and a distance of ~0.1–0.7 nmi from the capture location. Locations of these fish were determined over the next 2.5 days during three periods between submersible operations. The fish were scattered along a 1.1 nmi east-west axis (Fig. 6). Most fish demonstrated short-term movements of over 0.1 nmi (our nominal error of navigation) during these 2.5 days. Two fish (23 and 28) moved ~0.5 nmi. Only one fish (22) ended up near the location where it was initially found on this cruise. None of these eight fish was found closer than 0.1 nmi to the original capture site, and most were 0.4 nmi away. There was no evidence that these fish stayed in a common school or within a small home range, as found earlier in the summer.

Vertical movements

Pressure-telemetering (depth sensor) transmitters were used during 1989 and 1990, but due to problems with the receiver, limited data were obtained. Figure 7 shows the maximum and minimum depths for 10-min intervals for three fish monitored almost continuously during 21–22 and 24–25 August 1989. Fish were usually in midwater, inhabiting depths of 25–50 m where the bottom was ~75 m. Short-duration vertical movements were seen for all fish, usually rapid descent/ascent ("bounce") dives to or close to the bottom, followed by rapid vertical ascents back to depths of 25–35 m. Fish 2 made nine of these "bounce dives" to the bottom during the early morning of 24 August over about a 4 h period. Other than this series of dives, there was little evidence for any diel patterns in the frequency of vertical migrations of fish that were tagged. Fish 3 either regurgitated its transmitter or rested on the bottom after 0700 h on 25 August (Fig. 7).

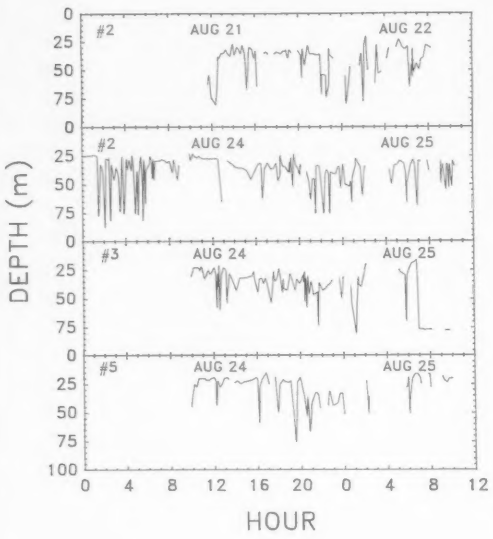


Figure 7
Depths of yellowtail rockfish *Sebastes flavidus* nos. 2, 3, and 5 measured with pressure-telemetering transmitters during 21–25 August 1989. Bottom depths 75–99 m during this period.

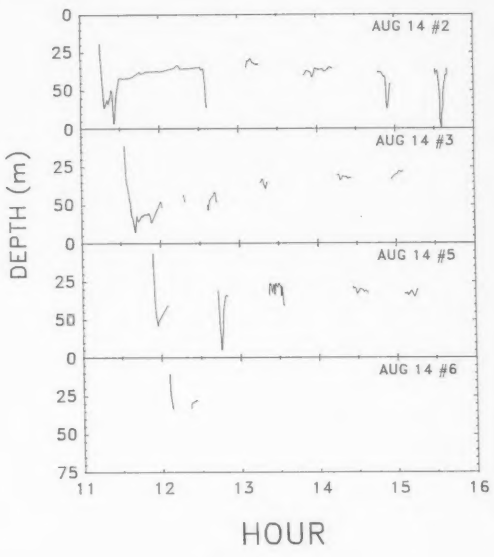


Figure 8
Depths of yellowtail rockfish *Sebastes flavidus* nos. 2, 3, 5, and 6 measured with pressure-telemetering transmitters during 14 August 1990. Bottom depths 75–80 m.

Vertical excursions of fish during late morning and afternoon of August 1990 showed a similar pattern, with fish occupying midwater depths and occasionally diving to deep water (Fig. 8). The records for Fishes 2 and 3 show that these fish descended toward the bottom immediately after release and then rose to progressively shallower depths during the next several hours. Synchronous vertical movements of several fish were not common (Figs. 7, 8) but some did occur among the three fish tracked during 25 August 1990 (Fig. 8). Sometimes fish dove as the vessel approached, perhaps a response to ship noise (Ona and Godoe 1990), but at other times fish descended when the vessel was not underway.

Maximum rates of descent for fish shown in Figure 8 were 0.16–0.40 m/sec; maximum ascents were 0.15–0.31 m/sec. Figure 9 shows the dive of Fish 5 after release, with the most rapid descent during the first minute, and slower rates in the next 3 minutes. Rapid vertical movements were also observed during 1989, with maximum rates of descent of 0.15–0.45 m/sec, and rates of ascent of 0.15 m/sec.

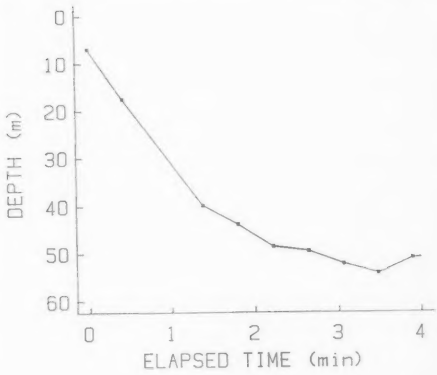


Figure 9
Initial descent of yellowtail rockfish *Sebastes flavidus* no. 5, starting at 1154 h, 14 August 1990, after release at the surface (see Fig. 8).

Discussion

Homing and horizontal movements

During all three years of the study, yellowtail rockfish on Heceta Bank demonstrated site fidelity and homing. Displaced fish returned from as far as 2 nmi from their capture site, and those released over rocky habitat and at similar depths returned to the location of capture in 1990. Eleven of twelve fish tagged in 1990 returned to or remained close to the original capture site 13 days after release. One fish that was displaced 0.5 nm returned overnight to the location where it was captured.

Carlson and Haight (1972) also found that adult yellowtail rockfish returned to their home site, some from as far as 22.5 km, some after displacement to other yellowtail schools, and some after 3 months in captivity. In both studies, yellowtail rockfish homed even if released at sites where the habitat was similar to that at the capture site and near other schools of yellowtail rockfish. This demonstrates fidelity to a home site.

Not all yellowtail rockfish demonstrate site fidelity, however. Eight of ten recoveries of 153 yellowtail rockfish tagged in Puget Sound were from the open Washington coast, 58–2214 days after release, indicating an offshore migration probably related to the onset of maturation of these fish (Mathews and Barker 1983). In another study, Stanley (1988) tagged 4622 yellowtail rockfish in Queen Charlotte Sound, British Columbia during 1980 and 1981. As of 1987, the five that were recovered moved from <10 km to >300 km. Of 9417 yellowtail rockfish tagged southwest of Vancouver Island, 24 were recovered. Twelve moved <10 km while others were recovered 23 to >500 km from the tagging location (Stanley 1988).

The degree of site fidelity and movement of yellowtail rockfish may be related to the bottom topography of the tagging location. This appears to be the case for black rockfish, another offshore pelagic species. Culver (1987; B.N. Culver, Wash. Dep. Fish., Montesano, pers. commun.) found that black rockfish tagged over a 5-year period from rocky habitats of northern Washington exhibited "no significant movement," whereas fish tagged in areas that had sandy sediments or small pinnacles off the central Washington and northern Oregon coast displayed appreciable movements. Perhaps yellowtail rockfish on Heceta Bank, and other rocky banks, are less mobile than those inhabiting areas with level seafloors.

Carlson and Haight (1972) found that fish displaced to sites across open water with depths >100 m returned to the site of capture with much less frequency than did fish released along the adjacent coast in shallower depths. One fish in my study, released in relatively deep water off Heceta Bank and tracked continuously for 14 hours (Fish 4, Fig. 3), was not oriented toward its home site. These observations suggest that homing is most effective over relatively shallow water (<100 m), even though yellowtail rockfish are basically midwater fish. Homing may also be influenced by topography. Matthews et al. (1987) reported that displaced copper and quillback rockfishes *S. caurinus* and *S. maliger* returned to high-relief, but not to low-relief, reefs.

The sensory mechanisms and environmental cues used for homing and home-site recognition by yellowtail rockfish are not known. Possibly the fish on Heceta Bank recognized familiar topography and prominent "landmarks." Movements of up to 0.75 nmi by yellowtail rockfish (Figs. 5 and 6) indicate that they do not always have as small a home range and may range over a large portion of the bank. Perhaps they learn visual "landmarks" over much of the bank in this way.

One fish returned to its home site from 925 m after only 11 hours, mainly during the night when recognition of visual landmarks would have been more difficult. This fish returned home more rapidly than substrate-associated copper and quillback rockfishes that took 8–25 days to return home after displacement of only 500 m (see Matthews 1990 for this and summary of homing by other rockfishes). This suggests oriented or directed movement.

Eight of the twelve fish tagged in August 1990 were relocated 1 month after release but were all south of the capture location and scattered in an east-west direction. None was found within 0.1 nmi of the capture site. This dispersal from the capture site suggests reduced site fidelity and perhaps seasonal dissociation of individuals from the large schools observed earlier during the summer. This dispersal may be associated with seasonal changes, perhaps related to mating behavior and the fact that most of the fish tagged were large males. Carlson and Barr (1977) reported that the spatial distribution and activity of yellowtail and dusky (*S. ciliatus*) rockfishes differed markedly between May–October, when they were seen in the water column and apparently actively feeding, and November–April, when they withdrew into crevices between boulders. Although no distinct seasonal changes are known in the bathymetric distribution of yellowtail rockfish (J. Tagart, Wash. Dep. Fish., Olympia, pers. commun., Aug. 1991), the spatial distributions of other species of rockfishes are known to change seasonally (Miller and Geibel 1973, Patten 1973, Matthews et al. 1987). Several species of juvenile rockfishes are known to move to deeper reefs with the onset of fall and winter storms (Love et al. 1991). It would be interesting to learn if the yellowtail rockfish of Heceta Bank disperse and become more benthic during the late fall and winter, and then if they eventually regroup at the original capture location next spring after spawning, or instead acquire new home sites on the bank. Studies are obviously needed on seasonal and long-term movements of yellowtail rockfish.

Diel vertical movements

Most yellowtail rockfish were seen swimming above the bottom during submersible dives on Heceta Bank. However, a few were observed resting on the sea floor. More fish were observed inactive on the bottom during night than day dives. The tagged yellowtail rockfish of Heceta Bank were pelagic, swimming far above the

bottom most of the time. Data from pressure-telemetering tags show that fish dove toward the bottom but remained there only briefly. Only one fish with a pressure transmitter either rested on the bottom for an extended period or disgorged its transmitter (Fig. 7).

Little is known about the diel vertical distribution of rockfishes. Schools of *S. entomelas* and *S. proriger* are known to rise off the bottom during the night and become more diffuse than dense schools on the bottom during the day (Leaman et al. 1990). Rockfish may intercept vertically-migrating pelagic organisms that constitute their primary prey, feeding closer to the surface at night or during crepuscular periods and descending with their prey during the day. Sometimes vertically migrating prey, such as euphausiids, are advected onto banks and seamounts and trapped near the bottom during the day where they are devoured by rockfishes (Isaacs and Schwartzlose 1965, Chess et al. 1988, Genin et al. 1988, Hobson 1989). Euphausiids are often the primary prey of adult yellowtail rockfish (Lorz et al. 1983). About 50% of the diet by weight of yellowtail rockfish from Heceta Bank was comprised of euphausiids (Brodeur and Pearcy 1984). However, vertically-migrating mesopelagic fishes and shrimp were the primary food items of yellowtail rockfish collected in deeper water (137 m bottom depth) along the southern edge of Astoria Canyon (Pereyra et al. 1969).

Yellowtail rockfish from Heceta Bank did not demonstrate obvious diel changes in their behavior by either rising closer to the surface at night or swimming over deeper water to intercept more oceanic organisms. Such behavior has been observed for other species of rockfishes (Chess et al. 1988, Leaman et al. 1990), and predatory shore fishes are known to migrate offshore at night to feed in midwater (Hobson 1968). One yellowtail rockfish on Heceta Bank with a pressure-telemetering transmitter made more dives to the bottom during night than day.

The reasons for dives to the bottom are unclear. One possible explanation is that these dives assist the fish in localizing their position on the bank and preventing drift of the school away from their home station. Surface currents often set the ship away from tagged fish that appeared to be geostationary. Yellowtail rockfish must be able to orient to a specific site and swim against prevailing currents to maintain their position.

Tagging-tracking techniques

Sonic tags inserted into the stomachs of yellowtail rockfish without retention hooks were useful for tracking fish for several days. Most fish showed detectable movements up to 2 days after release. Horizontal movements greater than the accuracy of fixes were found in one fish 10 days later, but this was an exception. Depth sensor tags provided reliable information on the retention of tags since fish were almost always in midwater. Fish with depth transmitters remained in midwater up to 5 days, the rated duration of the batteries. One pressure-sensitive tag (Fish 3, Fig. 7) was apparently regurgitated after 22 h and fell to the bottom. If ARM's were employed on tags, fish movements were measurable for 1 month after release. One ARM tag dropped to the bottom immediately after the fish was released, demonstrating that restraining hooks are not a guarantee that tags will stay in the stomach. Eight of the twelve fish with non-pressure telemetering ARM tags that were relocated moved significant distances 30 days after the release of fish, indicating long-term retention of transmitters.

Effects of the transmitter on behavior of the fish are not known. However, one fish apparently schooled soon after release. Although fish dove toward the bottom immediately after release, they rose to typical midwater depths after less than an hour. These observations suggest that the trauma of being caught, tagged, and released, and the added weight of the transmitter, did not have prolonged effects and tagged fish behaved normally.

Acknowledgments

This research was supported by the Department of Interior's U.S. Minerals Management Service (Cooperative Agreement 14-12-0001-30445). NOAA's National Undersea Research Program provided supplemental shiptime and submersible support. I thank J.P. Fisher, B.N. Tissot, R. Albright, and the Captain of the FV *Corsair*, W. Dixon, and his crew for conducting this research at sea, J.P. Fisher for his help with analyses of the data, and J.P. Fisher, A. Schoener, M.A. Hixon, and two anonymous reviewers for helpful comments on the manuscript. A. Ebeling and M.A. Hixon provided the microgasometer and advice to determine the composition of gas escaping from decompressed yellowtail rockfish.

Citations

Brodeur, R.D., and W.G. Pearcy
1984 Food habits and dietary overlap of some shelf rockfishes (genus *Sebastes*) from the northeastern Pacific Ocean. Fish. Bull., U.S. 82:269–293.

Carlson, H.R.
1986 Restricted year-class structure and recruitment lag within a discrete school of yellowtail rockfish. Trans. Am. Fish. Soc. 115:490–492.

Carlson, H.R., and L. Barr
1977 Seasonal changes in spatial distribution and activity of two species of Pacific rockfishes, *Sebastes flavidus* and *S. ciliatus*, in Lynn Canal, southeastern Alaska. Mar. Fish. Rev. 39(3):23–24.

Carlson, H.R., and R.E. Haight
1972 Evidence for a home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish. Res. Board Can. 29: 1011–1014.

Chess, J.R. , S.E. Smith, and P.C. Fischer
1988 Trophic relationships of the shortbelly rockfish, *Sebastes jordani*, off central California. Calif. Coop. Oceanic Fish. Invest. Rep. 29:129–136.

Culver, B.N.
1987 Results from tagging black rockfish (*Sebastes melanops*) off the Washington and northern Oregon coast. *In* Proc., Int. rockfish symp., p. 231–239. Univ. Alaska Sea Grant Rep. 87-2, Fairbanks.

Dugan, R.F., and D.A. Dashin
1979 How to get the most out of LORAN-C. Oregon State Univ. Ext. Mar. Advis. Prog. SG-54, Corvallis, 12 p.

Eldridge, M.B., J.A. Whipple, M.J. Bowers, B.M. Jarvis and J. Gold
1991 Reproductive performance of yellowtail rockfish, *Sebastes flavidus*. Environ. Biol. Fish. 30:91–102.

Genin, A., L. Haury, and P. Greenblatt
1988 Interactions of migrating zooplankton with shallow topography: Predation by rockfishes and intensification of patchiness. Deep-Sea Res. 35:151–175.

Gunderson, D.R., P. Callahan, and B. Goiney
1980 Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3):74–79.

Hixon, M.A., B.N. Tissot, and W.G. Pearcy
1991 Fish assemblages of rocky banks of the Pacific Northwest. Final Rep. to U.S. Dep. Int., Minerals Manage. Serv., MMS 91-0052, Oregon State Univ., Corvallis, 409 p.

Hobson, E.S.
1968 Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish. Wildl. Serv. Res. Rep. 73, 92 p.
1989 Predation on ocean krill. Science (Wash. DC) 243:237.

Isaacs, J.D., and R.A. Schwartzlose
1965 Migrant sound scatterers: Interaction with sea floor. Science (Wash. DC) 150:1810–1813.

Leaman, B.M., R. Kieser, P. Withler and R.D. Stanley
1990 *W.E. Ricker* hydroacoustic cruise to study rockfish behavior off northern Vancouver Island, March 14–23, 1990. Can. Manuscr. Rep. Fish. Aquat. Sci. 2091, 63 p.

Lorz, H.V., W.G. Pearcy, and M. Fraidenburg
1983 Notes on the feeding habits of the yellowtail rockfish, *Sebastes flavidus*, off Washington and in Queen Charlotte Sound. Calif. Fish Game 69:33–38.

Love, M.S.
1979 Isolation of olive rockfish, *Sebastes serranoides*, populations off southern California. Fish. Bull., U.S. 77:975–983.

Love, M.S., P. Morris, M. McCrae, and R. Collins
1990 Life history aspects of 19 rockfish species (Scorpaenidae: *Sebastes*) from the southern California Bight. NOAA Tech. Rep. NMFS 87, 38 p.

Love, S.M., M.H. Carr, and L.J. Haldorson
1991 The ecology of substrate-associated juveniles of the genus *Sebastes*. Environ. Biol. Fish. 30:225–243.

Mathews, S.B., and M.W. Barker
1983 Movements of rockfish (*Sebastes*) tagged in northern Puget Sound, Washington. Fish. Bull., U.S. 82:916–922.

Matthews, K.R.
1990 A telemetric study of the home ranges and homing routes of copper and quillback rockfishes on shallow rocky reefs. Can. J. Zool. 68:2243–2250.

Matthews, K.R., B.S. Miller, and T.P. Quinn
1986 Movement studies of nearshore demersal rockfishes in Puget Sound, Washington. *In* Proc., Int. rockfish symp., p. 63–72. Univ. Alaska Sea Grant Rep. 87-2, Fairbanks.

Matthews, K.R., T.P. Quinn, and B.S. Miller
1990 Use of ultrasonic transmitters to track demersal rockfish movements on shallow rocky reefs in Puget Sound, Washington. *In* Parker, N., et al. (eds.), Fish marking techniques, p. 375–379. Am. Fish Soc. Symp. 7, Bethesda.

Miller, D.J., and J.J. Geibel
1973 Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Fish Game Fish Bull. 158, 137 p.

Ona, E., and O.R. Godoe
1990 Fish reaction to trawling noise: The significance to trawl sampling. *In* Karp, W.A. (ed.) Developments in fisheries acoustics: A symposium held in Seattle, 22–26 June 1987. Rapp. P.-V. Reun. Cons Int. Explor. Mer 189:159–166.

Pacific Fisheries Management Council
1991 Status of the Pacific coast groundfish fishery through 1991 and recommended acceptable biological catches for 1992. Pac. Fish. Manage. Counc., Portland, 69 p.

Patten, B.G.
1973 Biological information on copper rockfish in Puget Sound, Washington. Trans. Am. Fish. Soc. 102:412–416.

Pearcy, W.G., D.L. Stein, M.A. Hixon, E.K. Pikitch, W.H. Barss, and R.M. Starr
1989 Submersible observations of deep-reef fishes of Heceta Bank, Oregon. Fish. Bull., U.S. 87:955–965.

Pereyra, W.T. , W.G. Pearcy, and F.E. Carvey
1969 *Sebastes flavidus*, a shelf rockfish reeding on mesopelagic fauna, with consideration of ecological implications. J. Fish. Res. Board Can. 26:2211–2215.

Scholander, P.F., L. Van Dam, C.L. Claff, and J.K. Kanwisher
1955 Micro gasometric determination of dissolved oxygen and nitrogen. Biol. Bull. (Woods Hole) 109:328–334.

Stanley, R.D.
1988 Shelf rockfish (silvergray, yellowtail, and canary rockfish. *In* Fargo, J., et al. (eds.), Groundfish stock assessments for the west coat of Canada in 1987 and recommended yield options for 1988, p. 227–272. Can. Tech. Rep Fish. Aquat. Sci. 1617.

Stasko, A.B., and D.G. Pincock
1977 Review of underwater biotelemetry, with emphasis on ultrasonic techniques. J. Fish. Res. Board Can. 34:1261–1285.

A simple simulation approach to risk and cost analysis, with applications to swordfish and cod fisheries

Victor R. Restrepo
University of Miami, Rosenstiel School of Marine and Atmospheric Science
4600 Rickenbacker Causeway, Miami, Florida 33149

John M. Hoenig
Department of Fisheries and Oceans, Science Branch
P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada

Joseph E. Powers
Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA
75 Virginia Beach Drive, Miami, Florida 33149

James W. Baird
Department of Fisheries and Oceans, Science Branch
P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada

Stephen C. Turner
Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA
75 Virginia Beach Drive, Miami, Florida 33149

Abstract.–Monte Carlo simulation is used to quantify the uncertainty in the results of sequential population analysis and related statistics. Probability density functions describe the measured or perceived uncertainty in the inputs to the assessment model. Monte Carlo simulation is then used to examine the variability in the resulting parameter estimates (stock sizes and fishing mortalities), derived statistics (e.g., $F_{0.1}$), and in the management regulations necessary to achieve various management objectives. We show how relative frequency histograms of the simulation results can be used to describe the risk of not meeting a given management goal as a function of the catch quota selected. We also show how to compute the expected cost, in terms of potential yield foregone, associated with picking a conservative quota. This enables one to balance risks and costs or to allow risk to vary within proscribed limits while keeping the catch quota stable. We illustrate the use of the Monte Carlo approach with examples from two fisheries: North Atlantic swordfish and northern cod.

Manuscript accepted 29 July 1992.
Fishery Bulletin, U.S. 90:736–748 (1992).

Fishery managers recognize the dangers of accepting parameter estimates without consideration of the variability inherent in the estimates of fish stock status and related parameters. Early strategies for dealing with this were quite simple, such as replacing the estimate of the fishing mortality giving the maximum yield (F_{max}) by a more conservative value. Sensitivity analyses, in which the effects of various perturbations of the inputs are observed, have commonly been employed to obtain impressions of the probable bounds on the errors (e.g., Pope 1972, Pope and Garrod 1975). Recently, various authors have used the delta method (see Kendall and Stuart 1977: 246–248) to obtain analytical expressions or numerical solutions for the variances and covariances of outputs from simple sequential population analyses (SPAs) (Saila et al. 1985, Sampson 1987, Prager and MacCall 1988, Kimura 1989). These solutions tend to be complex, only asymptotically valid, and highly model-specific. They have only been worked out for the simplest SPA models and some simple quota-setting procedures (e.g., Pope 1983).

It is possible to measure how well the population estimates correspond to trends in indices of abundance when calibration procedures are applied to sequential population analyses. The variance-covariance matrix of the stock sizes estimated directly in the optimization procedure is calculated from the inverse Hessian or its approximation (Seber and Wild 1989); the variance of any function of these parameters is then approximated by the delta method. But estimates of standard errors of population sizes obtained in this way do not reflect all the variability in the inputs and the uncertainty in the model, because they are conditioned on a number of assumptions such as natural mortality being exactly

known. For example, similar trends in population abundance may be obtained when two very different values of natural mortality rate are assumed as inputs; despite the similar trends (and hence correlation with the abundance indices), there may be large differences in the absolute estimates of abundance.

In this paper we use the term "uncertainty" to describe any variability or error that arises during the stock assessment process. Uncertainty can enter into an assessment in various ways. There may be uncertainties in the values of the inputs, e.g., the total catch may be estimated with error. Also, the formulation of the assessment model may be subject to uncertainty, and the analyst may make data-dependent decisions during the analysis which are subject to error. The degree to which these sources of error are incorporated into the analyses will determine the perceived uncertainty in the overall assessment results. If all sources of error are not appropriately accounted for, then estimates of the uncertainty in the assessment results may be too small.

Monte Carlo simulation is a convenient tool for studying a model's outputs given different types and levels of error in the model's inputs (e.g., Restrepo and Fox 1988). In a sensitivity analysis framework, Pope and Gray (1983) and Rivard (1983) used a Monte Carlo approach to study the relative contribution of various inputs to the overall uncertainty in total allowable catch (TAC) estimates obtained from calibrated SPAs. Francis (1991) used Monte Carlo simulation analysis to construct risk curves describing the chances of not meeting management objectives as a function of the catch quota. In this paper, we present a general method, also based on Monte Carlo simulation, to account for uncertainty in assessment results, including the parameters directly estimated from the SPAs as well as derived statistics used to set management targets and allowable catches. We also show how the simulation results can be used to quantify the risk (of not meeting a management goal) associated with the selection of a given TAC, and we describe a measure of the cost of picking a conservative catch quota.

We apply the simulation method to swordfish *Xiphias gladius* in the North Atlantic Ocean and cod *Gadus morhua* off eastern Newfoundland and southeastern Labrador. These fisheries are quite different in nature. Swordfish are highly migratory, managed internationally with fishing mortality controls, and the data set allows for the estimation of only a few parameters in models with many constraints. Northern cod, on the other hand, are demersal, managed by quota, and the availability of age-specific survey indices allows for the estimation of many parameters with a minimum number of assumptions.

Quantifying uncertainty by simulation

Suppose the only uncertainty in the inputs to an assessment model concerns the value of the instantaneous natural mortality rate, M, and that M could be anywhere in the interval 0.15–0.25/yr with equal likelihood. One could compute the assessment model results for a large number of uniformly spaced values of M in this interval (e.g., 100) and make histograms of the results. This would represent the perceived information about the relative likelihood of the estimated output taking on various values. If not all values of M were believed to be equally likely, one could weight the 100 outputs by the probability associated with the corresponding inputs.

The above procedure becomes awkward when there are a number of inputs subject to uncertainty, because the number of combinations of input parameter values becomes very large. An alternative is to use a Monte Carlo approach in which values of the inputs are drawn randomly from probability distributions. A sufficiently large number of plausible input data sets are thus generated and used to compute the assessment model results such that the distributions of the estimated outputs are clearly defined. This may involve hundreds or thousands of runs, depending on the types of data and models used (in our work we found that 500–1000 data sets were necessary to obtain stable results).

A typical assessment of a fish stock using SPA involves three levels of analysis. First, data are prepared for the SPA. This usually involves estimating and ageing the annual catch, and computing indices of abundance for calibration. Second, the SPA itself is carried out (it is also frequently termed "VPA," for Virtual Population Analysis). In many cases, several SPAs are carried out to examine the goodness-of-fits of the input data to alternative model formulations or simply to examine the sensitivity of the results to the alternative formulations. Third, derived statistics are computed. These are commonly biological reference points (F_{max}, $F_{0.1}$; Gulland and Boerema 1973), and forward projections of stock status and catches under alternative management actions.

It is easy to see how the Monte Carlo approach can be used to characterize the uncertainty in the entire analysis process, starting with the raw data collected for the first step in the above procedure. For instance, the total annual catches and their proportions at age can be obtained by resampling the original data that led to the catch estimates, through a non-parametric bootstrap (Efron 1982). These bootstrapped catches would then be used in the SPAs, whose results, in turn, would affect the values of projected future catches.

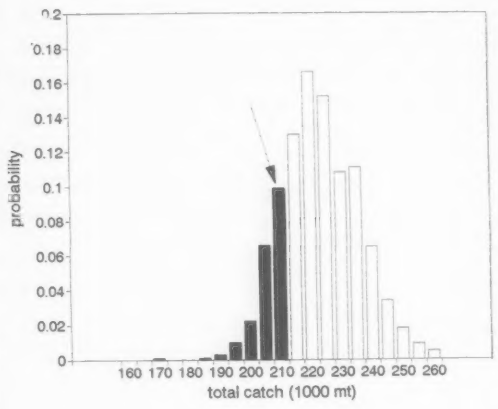


Figure 1

Probability mass distribution (relative frequency) for estimates of total catch of cod *Gadus morhua* necessary to have 1991 fishing mortality equal to that of 1990. Estimates were obtained from 1000 simulated data sets analyzed by the ADAPT approach. If a total catch of 210,000 mt is selected (arrow), the probability that fishing mortality will exceed the status quo is estimated by the sum of histogram bar heights to the left of 210,000 (i.e., the shaded portion).

In practice, however, the time and computer resources required to carry out such a large-scale simulation make it more practical to derive the input uncertainty distributions from parametric statistical analyses of data. This would involve assuming a distribution type for the inputs and estimating their mean and variance. For example, by virtue of the central limit theorem, an estimated mean has an approximately normal distribution if the sample size is sufficiently large.

Often, the distributions determined for some of the inputs will not be based on a rigorous statistical treatment of the data, but rather will represent educated guesses about the likelihood of the inputs taking on particular values (this is probably most true for the natural mortality rate, M, which is usually assumed and not estimated). The outputs would then represent the analyst's personal uncertainty in the assessment results.

The above approach can be generalized to allow for uncertainty in the formulation of the SPA model as well. Suppose one believes that there is a 70% chance that the fishing mortality rate in the last year does not decline with age after a fully recruited age (this is often known as a "flat-topped" partial recruitment curve), and a 30% chance that it does decline ("dome-shaped" partial recruitment). Then one could conduct 70% of the simulations with an SPA that assumes the flat-topped curve and 30% with the dome-shaped curve. The resulting combination of outputs would reflect the intuitive estimate of uncertainty about the SPA model formulation. Similarly, the approach can also account for uncertainty concerning data-dependent decision making. For example, if several abundance indices are available, one might subject each index to a preliminary test to decide whether the index is acceptable for calibrating the SPA, e.g., via analysis of residuals. One can repeat this decision-making process for each of the simulated data sets and thus account for the uncertainty associated with screening indices.

In summary, the Monte Carlo approach to quantifying uncertainty consists of generating a large number of pseudo-data sets, drawn at random from specified distributions, and carrying out *the entire assessment* procedure for each data set. The distributions of the assessment outputs and derived statistics are then summarized, e.g., as histograms. The simulation is thus viewed as a means for translating input and model uncertainties (measured and/or perceived) into output uncertainties.

Analyzing the consequences of management options

Estimating risks

The simulation results can also be used to quantify the uncertainty associated with a future management action. An example is the determination of uncertainty in the catch of the current year that would maintain the fishing mortality at the level of the previous year ($F_{status\ quo}$). A point estimate might be computed as follows. An SPA of some sort is used to estimate the population size at the end of the previous year and the fishing mortality during that year. Assuming that recruitment in the current year is equal to the long-term average, the estimated population size in the current year can be computed. Finally, the harvest which causes the population to experience the same fishing mortality rate as that estimated for the previous year can be computed. To quantify the uncertainty in this result, the whole procedure can be repeated 1000 times, each time perturbing each input to the SPA by a random amount (as per the specified uncertainty distributions). This results in 1000 sets of estimates of population size, fishing mortality, and natural mortality rate which, together with a set of randomly-drawn values for recruitment, can be used to generate 1000 estimates of the total allowable catch which will cause the fishing mortality to remain unchanged. These values can be organized into a relative-frequency histogram such as in Figure 1.

From the histogram, it appears that the most likely (modal) value for achieving the management goal

($F_{status\ quo}$) is a quota of 220,000 mt, but the actual value might be anywhere from ~170,000 to 260,000 mt. If the TAC is set at 220,000 mt, then these results suggest there is roughly a 50% chance of the fishing mortality increasing and a 50% chance of it decreasing. Suppose one is risk averse and chooses a TAC of 210,000 mt instead. What would be the perceived risk, or probability of exceeding the target fishing mortality, under this quota?

The risk of exceeding the target fishing mortality ($F_{status\ quo}$) is given by the proportion of the area under the histogram to the left of the TAC chosen (Fig. 1). Thus,

$$\text{Prob}(F_{achieved} > F_{target}) = \sum_{i=1}^{I} p(i)$$

where p(i) is the probability mass (relative frequency of outcomes) associated with the ith bar of the histogram, and I is the number of bars to the left of the chosen TAC. This probability can be computed for any value of the TAC. In practice, the risk would be computed by sorting in ascending order the 1000 catch values obtained from the simulation, and then plotting the cumulative count of outcomes less than any value of the TAC versus that value of the TAC (Fig. 2). One can also derive a family of risk curves. For example, separate curves could be generated for the risk of exceeding $F_{status\ quo}$ by each of several amounts (in absolute or relative numbers). For each of the 1000 simulation runs, one computes the value of $F_{status\ quo}$ and the catch that causes current F to exceed the status quo by the specified amount. The resulting histogram of catches is summed to obtain the risk curve.

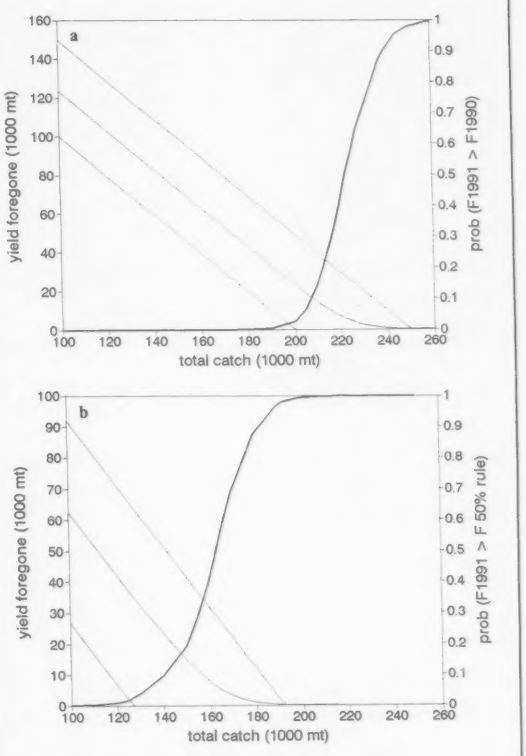


Figure 2

(a) Probability of exceeding the current (1990) cod *Gadus morhua* fishing mortality and expected value of the potential yield foregone (with 95% confidence band determined as the 2.5th and 97.5th percentiles of the distribution resulting from 1000 simulations) as functions of total catch selected for 1991. (b) Probability of the 1991 fishing mortality exceeding the 50% rule fishing mortality, and expected value of the yield foregone (with 95% confidence band), as functions of the total catch selected for 1991.

Estimating cost as yield foregone

If we choose a conservative value for the TAC in order to ensure that risk of exceeding the target fishing mortality will be small, then we are probably passing up some of the yield we could have had in the short term while still meeting our objective (e.g., see Bergh and Butterworth 1987). It is possible to describe this cost in economic or biological terms. Here, we express the cost as the expected value of the potential yield foregone, which we define as follows. For any TAC, x, let

$$\delta(i) = \begin{cases} 0, \text{ yield associated with ith interval of histogram} \leq x \\ 1, \text{ yield associated with ith interval of histogram} > x. \end{cases}$$

Then,

$$E(\text{potential yield foregone}) = \sum_{i=1}^{\infty} p(i)\,\delta(i)\,(y(i) - x)$$

where E(||) denotes the expectation operator, the summation is over all intervals of the histogram (Fig. 1), and

y(i) is the yield associated with the ith interval of the histogram. The expected potential yield foregone can be plotted against the corresponding TAC (Fig. 2). Here, y(i)−x is a possible value of the yield foregone provided it is non-negative; negative values are eliminated by the indicator function δ(i); p(i) is the probability that the yield foregone is equal to δ(i) (y(i)−x). In practice, the expected yield foregone would be computed by setting all simulated catches which are less than the TAC equal to zero and then computing the mean of the 1000 values minus the TAC. The results can then be plotted versus the TAC for various choices of TAC (Fig. 2).

It should be noted that this cost relates to the upcoming year only. One can also calculate the fate of the biomass left in the water at the end of the upcoming year. That is, one can ask whether this biomass left in the water will increase or decrease over the year. In general, for a quantity of biomass left in the water, the relative change in its biomass over the year is given by

relative change in unfished biomass =

$$e^{-M}\frac{\sum_{a} P_a W_{a+1}}{\sum_{a} P_a W_a} - 1.$$

Here, P_a is the proportion of the stock that is age a; W_a, the average weight of animals at age a; M, the (constant) instantaneous natural mortality rate; and the summations are over all age groups of interest.

Trade-offs in decision making

The manager can now choose how to trade off potential yield and risk. For example, consider the option of a TAC of 210,000 mt as a means of maintaining the fishing mortality at a constant level. From Figure 2a, the perceived risk of the fishing mortality exceeding the target mortality is ~14%. The expected value of the potential yield foregone for this TAC is ~14,000 mt. If, instead, a TAC of 215,000 mt is selected, the risk of exceeding the target fishing mortality becomes 26% and the expected value of the potential yield foregone becomes 10,000 mt. Thus, an increase in the TAC of 5,000 mt would almost double the risk of exceeding $F_{status\ quo}$ while reducing the expected potential yield foregone by 30%.

Another way to present the results of the SPA simulations is to plot percentiles of output distributions versus the TAC selected. For example, for each SPA run on simulated data, one can take the estimated population size and iteratively seek the fishing mortalities that will result in each of several TACs. Then, for any value of TAC one can compute the median and 2.5th and 97.5th percentiles of the distribution of fishing mortalities. Since instantaneous fishing mortality may not be meaningful to some interested parties (such as fishing industry groups), one may wish to look at the distribution of changes in population biomass associated with particular choices of the TAC (Fig. 3).

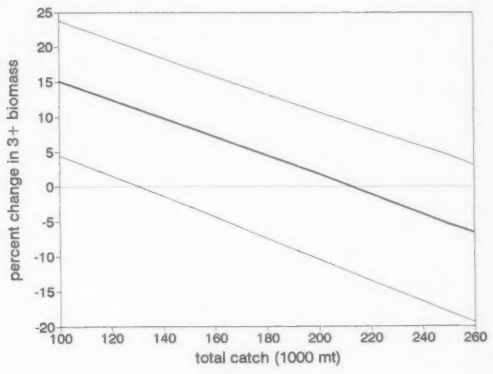


Figure 3

Percentiles of the distribution of relative change (%) in biomass of cod *Gadus morhua* age 3 and above, as a function of the total catch selected for 1991. Dotted lines: (top) 97.5th percentile; (middle) 50th percentile; (bottom) 2.5th percentile.

Thus, we have two approaches which we can summarize as follows. The first approach is to select a goal or objective (such as $F_{status\ quo}$ or $F_{0.1}$) and then quantify the chances of achieving that goal as a function of the TAC or effort restriction selected. The second is to quantify the consequences of choosing different quotas or effort restrictions. Both approaches are useful to managers. A manager might first ask how a specific management objective like $F_{0.1}$ can be met. A graph similar to Figure 2a makes it clear that the trade-off between risks and costs must be balanced. The manager might also want to know the consequences of picking particular quotas or effort restrictions. For example, for economic or political reasons, it may be difficult to stick with a management policy if a large quota reduction is called for. In this case, the consequences to the stock of maintaining the status quo or reducing the quota by various intermediate amounts may be of interest. A graph similar to Figure 3 may be helpful for this.

Managers and industry have a strong interest in maintaining stability in a fishery. Conflicts can easily arise when annual assessments provide only point estimates of the quota required to achieve a specified goal. This is because random error in the estimates

implies that annual adjustments in the quota will be proscribed even when no changes are in fact necessary. Instead of letting the quota "float" from year to year, one can stabilize the quota and let the risks float from year to year. Thus, as long as the risks remain within certain limits, there is no need to adjust the quota. (Here, the risks can include potential stock collapse as well as foregone potential yield.)

The sequential population analysis model: ADAPT

The examples presented below use data from two very different fisheries that are assessed with the same SPA approach, known as ADAPT (Gavaris 1988). ADAPT is widely used in the eastern United States and Canada. Here we describe the basic method briefly and direct the interested reader to more details in Parrack (1986), Gavaris (1988), Conser and Powers (1990), and Powers and Restrepo (1992).

The objective in ADAPT is to minimize deviations between observed (age-specific) indices of abundance and those predicted by what is commonly referred to as virtual population analysis (VPA). Let the subscripts t, a, and i denote time, age, and abundance-index sequence number, respectively. The basic equations governing the model are

$$N_{at} = N_{a+1,\,t+1}\, e^{Z_{at}}, \tag{1}$$

$$C_{at} = F_{at}\, N_{a+1,\,t+1}\, (e^{Z_{at}} - 1)/Z_{at}, \text{ and} \tag{2}$$

$$I_{it} = q_i\, N_{at}\, (1 - e^{-Z_{at}})/Z_{at}, \tag{3}$$

where N = stock size in numbers of fish, C = catch in numbers, I = index of relative stock abundance (each index is associated with one or more ages which must be specified), F = instantaneous fishing mortality rate, Z = total instantaneous mortality rate ($Z = F + M$), and q = coefficient of proportionality between relative abundance and absolute abundance. Inputs to the model are the catch, natural mortality, and relative abundance indices. Given that there are T years of data, A ages, and Y indices, a search algorithm, e.g., Marquardt-Levenberg (Seber and Wild 1989), is used to estimate the parameters q_i ($i = 1 \ldots Y$) and $N_{a,\,T+1}$ ($a = 2 \ldots A$) that minimize the weighted residual sum of squares:

$$RSS = \min \sum_i \sum_t \lambda_i\, (I_{it} - \widehat{I_{it}})^2, \tag{4}$$

where the weights, λ_i, may be input or estimated via iteratively-reweighted least squares.

ADAPT, like other VPA calibration procedures, requires model constraints in order to reduce the number of parameters. Hence, the stock sizes for the last age each year are not normally estimated but are instead derived from a specified relationship between F_{At} and $F_{A-1,\,t}$. Additional constraints may be required when the amount of relative-abundance data does not support the estimation of a large number of parameters. Often, as in the swordfish example below, this involves estimating the relative selectivities of the various age-groups in year T in some fashion external to the calibration process. This leads us to add to our explanation the notion that ADAPT is generally thought of as a framework rather than a rigid model. Thus the reader is likely to encounter applications that deviate from the model in equations (1) through (3). For example, for swordfish, A is a "plus" group consisting of ages A and older. For cod in Atlantic Canada, the objective function (4) is modified to allow for lognormal errors. A detailed presentation of some of the most commonly used options in ADAPT can be found in Powers and Restrepo (1992).

Assessment uncertainty: Application to North Atlantic swordfish

Swordfish in the North Atlantic Ocean are assessed by the International Commission for the Conservation of Atlantic Tunas (ICCAT). Interest is centered on the level of fishing mortality relative to reference values (e.g., F_{max}), and on trends in mortality and stock abundance. Potential management options involve restrictions aimed at controlling fishing mortality. The assessment procedure is continually changing as experience is gained. The procedure below was used for the 1989 assessment (ICCAT 1990).

Assessment procedure

Nine age-groups were recognized in the commercial catch, ages 1 to 9+. There were 11 years of catch-at-age data from 1978 to 1988. Fleets from the United States, Japan, and Spain accounted for most of the catch. Eleven abundance indices were available based on fleet-specific catch rates from the longline fisheries (ICCAT 1990).

Details of this assessment of the stock are presented in ICCAT (1990). Briefly, the procedure used was as follows. (1) A separable virtual population analysis, SVPA (Pope and Shepherd 1982), was computed in order to obtain estimates of the age-effects or partial recruitment in the last year for which data were available. Data from 1983 to 1988 were used for this under

the assumption that the selectivity pattern remained stable during that period. For that analysis the terminal fishing mortality was set to 0.2/yr and selectivity for the oldest age group was 3.0. (2) The ADAPT approach to sequential population analysis was then used for calibration, with each abundance index used separately. A weighting factor for each index was obtained by setting the weight for the ith index equal to the reciprocal of the mean squared error after calibrating with the index. In performing the calibrations, ages 5 and above were assumed to be fully recruited ($S_a = 1.0$ for $a = 5, 6, \ldots, 9+$) and the partial recruitment for the other ages was as determined from the SVPA (i.e., from step 1). (3) The set of weights computed for the abundance indices were then rescaled so that they summed to unity. (4) The weights were then used in recalibrating the ADAPT SPA using all of the abundance indices at once. In doing so, the following constraints were used: S_1 was taken from the separable virtual population analysis, S_2 through S_5 were directly estimated through calibration, and S_6 through S_{9+} were set equal to the estimated S_5. The objective function used in the calibration was to minimize the weighted sum of the squared deviations from the predicted abundance indices as in equation (4).

After the fishing mortalities and population sizes were computed by the sequential population analysis, the values of F_{max} and $F_{0.1}$ were calculated from yield-per-recruit computations. Data from the terminal year (i.e., the most recent year available) were used to project the catch in the current year and then project the catch for the next year. For this, recruitment in the current year and the following year were assumed by ICCAT to be equal to the long-term mean recruitment obtained in the sequential population analysis. The projections were made for a variety of fishing mortalities, specifically $F_{0.1}$, F_{max}, and $F_{status\ quo}$.

Specification of uncertainty in the inputs

One thousand simulated data sets were analyzed using a version of ADAPT written in FORTRAN 77 (available from the authors). The formulation of the problem was made to mimic the 1989 ICCAT assessment for North Atlantic swordfish. However, we emphasize that the uncertainties in the inputs specified below are our *ad hoc* choices and, although realistic, are intended mainly for illustrative purposes.

Natural mortality Uncertainty in the natural mortality rate (M) was specified as a uniformly-distributed random variable in the interval 0.1–0.3/yr. The value of 0.2 used by ICCAT (1990) is at the center of this range, and the choice of a uniform distribution places equal confidence in all values in the interval.

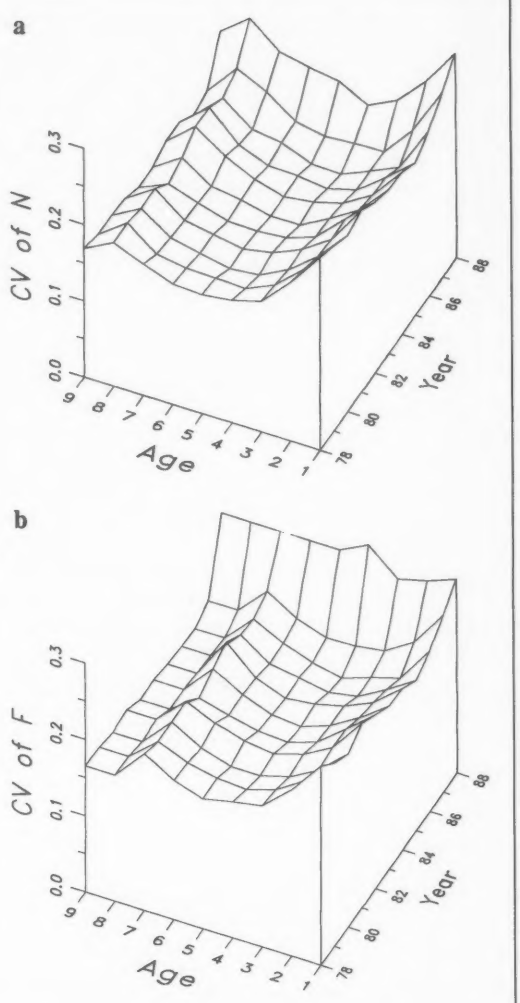


Figure 4
Coefficients of variation of outputs from the sequential population analyses of simulated swordfish *Xiphias gladius* data sets. (a) Age- and year-specific estimates of population numbers; (b) age- and year-specific estimates of instantaneous fishing mortality.

Catch-at-age Total annual catches were represented by lognormally-distributed random variables with coefficients of variation of 10% and expected values equal to those in the assessment. A coefficient of variation of 10% indicates that the catches are known with high precision. The proportions of the total catch in any year that make up each age component were assumed to follow a multinomial distribution with expected values

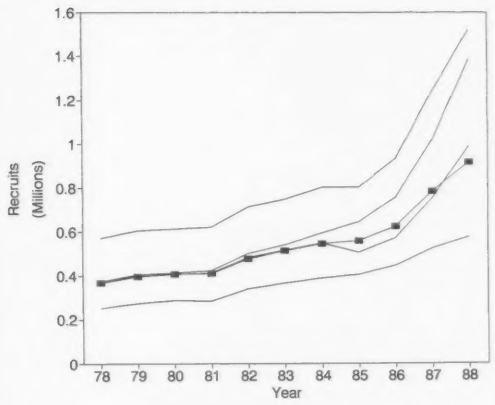


Figure 5

Distribution of swordfish *Xiphias gladius* recruitment estimates, by year, from the sequential population analyses. Outer lines are from the Monte Carlo simulations and show 95% confidence bands (determined as the 2.5th and 97.5th percentiles of the distribution resulting from 1000 simulations). Inner pair of lines shows confidence bands obtained from the information matrix after a single run of the ADAPT program using actual data. Line with symbols gives median estimate for each year from the simulations.

equal to the observed proportions and sample size equal to 1% of the annual catch. This model for the uncertainty was purely heuristic rather than based on measured variances.

Abundance (CPUE) indices The 11 available indices from the longline fisheries were also assumed to be lognormally distributed with a coefficient of variation of 10%. We chose a value of 10% as a rough approximation for all indices in all years. However, there is no reason why each index could not have a different coefficient of variation for each year depending on the amount of data available.

Results of swordfish simulations

The simulations gave rise to 1000 sets of age- and year-specific fishing mortality rates and population sizes. We computed the coefficient of variation of these sets of estimates for each age-year combination (Figs. 4a, b). As expected, the coefficients of variation were highest in the most recent year, 1988. Also, the age groups which form the bulk of the catch (ages 3–5) were the best determined. It is interesting to note that the coefficients of variation of fishing mortality rates for ages 8 and 9 were consistently lower than those for preceding ages. This is due to the manner in which the estimates for ages 8 and 9 were determined: it was assumed that $F_{8t} = F_{9t}$ (subscripts refer to age and year, respectively), and these were computed as a weighted average of fishing mortalities for ages 5–7. Thus, the uncertainty in the estimates of fishing mortality for the last two age-groups is solely a function of the uncertainties in the estimates for ages 5–7. This underscores the fact that the simulation results are conditional not only on the input-uncertainty distributions but on the formulation of the model being fitted as well.

The median recruitment (age 1) from the simulations increased over time (Fig. 5). However, the 95% confidence bands, defined by the 2.5th and 97.5th percentiles of the 1000 estimates, are quite wide. The confidence bands provided by the delta method for a single run with the actual data are much narrower than the ones obtained by the Monte Carlo approach. The former confidence bands indicate there is no uncertainty in the results for the converged part of the SPA in contrast to the simulation results. This is because the delta method results, based on the information matrix of a single run, are conditional on the natural mortality rate, catch at age, etc., being known exactly whereas the simulation accounts for uncertainty in these inputs. For this reason, we believe the simulation results are more reasonable.

Note that there appears to be very little interannual recruitment variability in the time-series (Fig. 5). This is probably due to the fact that fish ages were estimated from lengths deterministically by inverting the Gompertz growth equation, and this tends to blur the age-groups.

The population of fish age 5 and above appears to have declined rather steadily over time while the weighted fishing mortality rate appears to have increased (medians, Figs. 6a, b). Here, weighted fishing mortality is defined as the mean of the fishing mortality estimates for ages 5 through 9+, computed with weights proportional to the estimated population size at age. Again, the confidence bands are very wide.

It should be noted that for each run the estimates of fishing mortality, F_{at}, and population size, N_{at}, are highly correlated not only with each other but also with the value of natural mortality, M, used in the simulation run. For this reason, it is appropriate to examine trends in an estimated quantity one run at a time. We computed the ratio of the weighted fishing mortality in a given year t to the weighted F in the base year (taken to be 1978 in this example) for each simulation run (Fig. 7). The distribution of the fishing mortality ratio in 1979 was centered around 1.0; the ratio in 1986, 1987, and 1988 was >1.0 in 100% of the runs, thus clearly indicating that fishing mortality has increased. This result is not obvious from examination of Figure

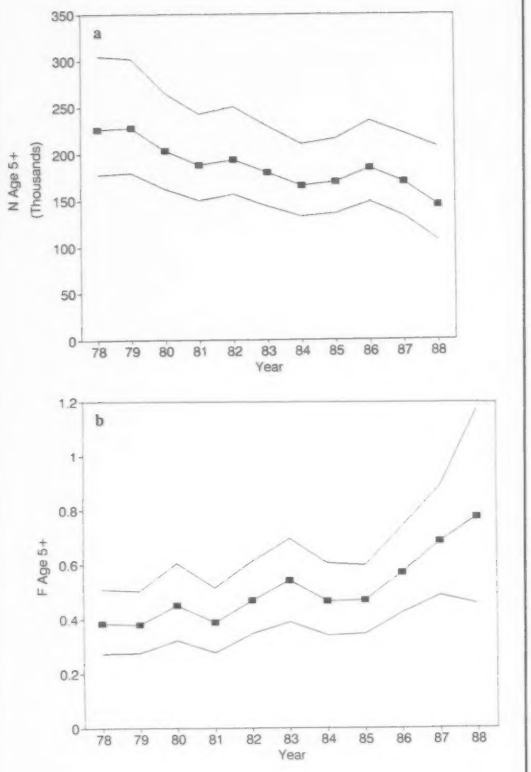


Figure 6

Medians, 2.5th percentiles, and 97.5th percentiles of the output distributions from the Monte Carlo simulations. (a) Distribution of estimates of the population size of swordfish *Xiphias gladius* aged 5 and above; (b) distribution of estimates of fishing mortality for swordfish aged 5 and above.

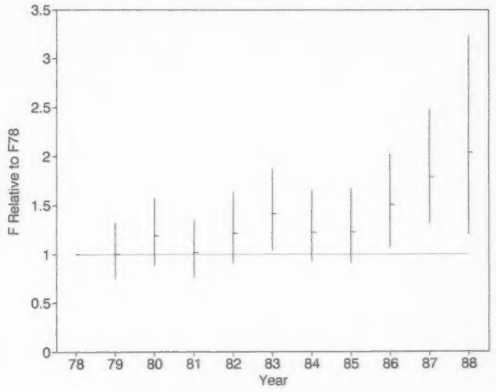


Figure 7

Distribution of the ratio of swordfish *Xiphias gladius* fishing mortality in year y to that in 1978 as a function of the year. Vertical bars indicate 95% confidence intervals based on percentiles; horizontal bars represent the median ratio.

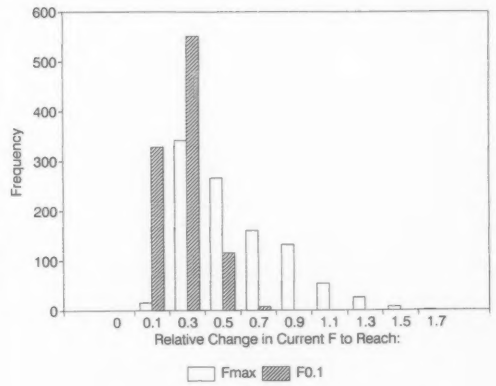


Figure 8

Multipliers necessary to bring the vector of age-specific fishing mortalities in the terminal year to the $F_{0.1}$ and F_{max} levels, for 1000 simulated data sets for swordfish *Xiphias gladius*.

6b and illustrates how very easily the Monte Carlo approach lends itself to hypothesis testing.

Of course, the goals of an assessment are not restricted to estimating population sizes and mortality rates. Interest is often centered on catch projections and quotas, effort regulations, and risk analyses. For swordfish assessments, it is useful to contrast the estimated current level of fishing mortality against reference points such as $F_{0.1}$ and F_{max}. The uncertainty in such comparisons (e.g., the ratio of current F to $F_{0.1}$) can easily be quantified using the Monte Carlo procedure. For each simulation run, we computed the multiplier that would be necessary to bring the estimated vector of age-specific fishing mortalities in the terminal year to the $F_{0.1}$ and F_{max} levels (Fig. 8). For the computations, we used the run-specific natural mortality rate and the weight-at-age relationships used by ICCAT in the 1989 assessment. No uncertainty was specified for weight relationships although this could easily be added if appropriate information were available. From Figure 8 it is evident that, to achieve the $F_{0.1}$ goal, fishing mortality must be cut to ~25% of its current value. With respect to F_{max}, it appears that fishing mortality must be cut by ~50% (Fig. 8). Note, however, that this conclusion is considerably less

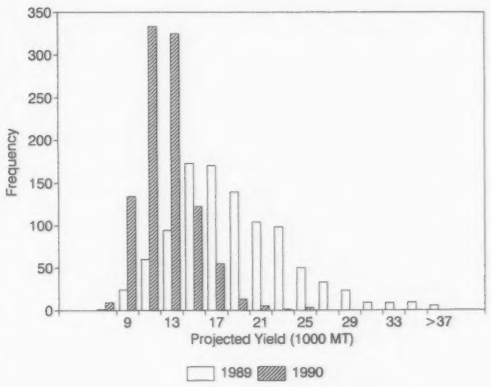


Figure 9

Distribution of 1989 estimated swordfish *Xiphias gladius* catches when fishing mortality is kept the same as in 1988 (open bars), and distribution of 1990 estimated catches when fishing mortality is equal to the midpoint between the 1988 fishing mortality and $F_{0.1}$, assuming 1989 fishing mortality was the same as in 1988 (cross-hatched bars).

certain than that for $F_{0.1}$ as evidenced by the fact that the distribution of multipliers is broader for F_{max} than for $F_{0.1}$. But, as an anonymous reviewer pointed out, it is interesting to note that the mode of both distributions is about one-third of the status quo F.

We also computed 1000 projected catches in weight for 1989 with fishing mortality equal to that in 1988. We then projected the catch for 1990 with fishing mortality set at the midpoint between the fishing mortality in 1988 and $F_{0.1}$ (Fig. 9). This method gradually reduces fishing mortality to minimize the short-term impact of decreased landings on fishermen (see Pelletier and Laurec 1990, for a discussion). Recruitments for 1989 and 1990 were drawn randomly from the empirical distribution of recruitments estimated from 1978–87 on each iteration. If the fishing mortality does not change in 1989 from the level in 1988, catches are likely to be somewhere around the 1988 yield of ~18,000 mt. The 1990 yields are likely to be ~11,000–13,000 mt.

Using the Monte Carlo results, it is equally simple to obtain distributions of catches for fishing at other exploitation levels or to obtain distributions of fishing mortalities for fixed catch quotas. Similarly, the distribution of other projected variables, such as the spawning-potential ratio that results from various catch and fishing mortality options, can be computed. In doing so, it is important to have the values of the inputs used in calibrating the SPAs (e.g., natural mortality) stored in each iteration, so that the projection computations use the same values.

Risks and costs: Application to northern cod

We studied the cod fishery in NAFO Divisions 2J+3KL and based our simulations on the data and methods described in Baird et al. (1990). Additional data, described below, were obtained from the files at the Northwest Atlantic Fisheries Centre, St. John's, Newfoundland. The simulations reflect our own perceptions and experience about the sources and nature of the uncertainties in the assessment. As with the swordfish example, the selection of management objectives for simulation was made for illustrative purposes.

This cod fishery is managed by quota. The assessment uses trawl-survey data and commercial catch-rate data to calibrate the SPA.

Assessment and simulation procedures

Only a brief description of the assessment procedure is given here since the details are not important for understanding the use of the simulation method. The catch-at-age data for ages 3–13 for each year from 1978 to 1989 were taken from Table 7 of Baird et al. (1990). Coefficients of variation of these catch estimates were computed using the method of Gavaris and Gavaris (1983); these coefficients were available in the files. The coefficients of variation ranged from 2 to 17%. Age- and year-specific catch rates from research-vessel surveys for the period 1978–89 and associated coefficients of variation (Baird et al. 1990, table 23) were used to tune the sequential population analysis. The coefficients of variation were ≤30% in 87% of the cases. Age- and year-specific catch rates from the offshore commercial trawl fishery for ages 5–8 for the period 1983–89 were standardized by the method of Gavaris (1980) for use as an index of abundance for tuning the SPA (Baird et al. 1990, table 39). We developed estimates of the coefficients of variation for the commercial catch-rate indices. In all cases, these were close to 10%. Natural mortality for this stock is believed to be around 0.2/yr.

In the simulations, the point estimates of the inputs were replaced by random variables with the same expected values and coefficients of variation as specified above. Catch at age values were generated as normal random variables, while the research-vessel and the commercial catch rates were generated as lognormal random variables. The value of the natural mortality rate was generated as a uniform random number between 0.15 and 0.25/yr.

The specific formulation of the ADAPT model was as follows. The research-vessel indices were obtained in the fall and were assumed to represent population size at the end of November. The commercial catch-rate indices were assumed to represent population size at the beginning of the year. The fishing mortality F for the oldest age-group (13) was calculated as 50% of the mean F for ages 7–9 weighted by population number at age. The objective function to be minimized differed from equation (4) in that lognormal errors were assumed and the weights, λ_i, were fixed to be 1.0.

Projections for 1990 and 1991 were made using the same procedures used in the most recent annual assessment (Baird et al. 1990). Population and fishing mortality projections for 1990 were made by randomly selecting a value for recruitment from the historical set of estimated recruitments and assuming that (1) the total catch in 1990 is 225,000 mt (the fixed Canadian quota in place when the assessment was done in 1990, plus an additional 25,000 mt in expected foreign catch), and (2) the partial recruitment (selectivity) vector for 1990 is equal to that estimated for 1989 in each simulated SPA.

Catch projections for 1991 were made in two ways. In one, we set the fishing mortality for 1991 equal to that for 1990 and solved for the catch. In the other, we set the fishing mortality for 1991 equal to

$$\min \{(\hat{F}_{0.1} + \hat{F}_{1990})/2,\ 2\ \hat{F}_{0.1}\}.$$

This is the 50% rule formulated by the Canadian Atlantic Fisheries Scientific Advisory Committee (Canada Department of Fisheries and Oceans 1991) for a gradual movement towards $F_{0.1}$. We also computed the fate of yield foregone and the distribution of population changes for various choices of the total catch.

Results of cod simulations

We generated risk curves for two fishing mortality objectives for 1991 (Figs. 2a,b). These curves can be put in perspective by noting that the Canadian total allowable catch for 1990 was 199,262 mt while the total catch (Canadian plus international) may have been as high as 235,000 mt. To have a 50% risk of increasing the fishing mortality in 1991 over the 1990 level, one would set the total catch at 225,500 mt; to have a 50% chance of exceeding the fishing mortality associated with the 50% rule would entail setting the total catch at 163,000 mt. It appears that a cut in the TAC would be necessary to have a reasonable chance of preventing the fishing mortality from exceeding the 1990 value. Substantial cuts in the harvest would be required to ensure a high probability of meeting the 50% rule.

For values of the TAC for which the risk is less than 25%, the expected value of the yield foregone is approximately a linear function of the TAC (Figs. 2a,b). That is, for every change in the TAC of 1000 mt, the expected yield foregone changes by ~1000 mt. The fate of biomass left in the water is to increase by ~13% in a year (mean of 1000 simulations = median = 12.9%; 95% confidence band based on 2.5th and 97.5th percentiles is 7.2% and18.4%). The relative change in biomass of fish aged 3 and above is also a linear function of the TAC (Fig. 3). Note, however, that the relative change in biomass cannot be determined very precisely as evidenced by the wide confidence bands.

We presented results of catch projections for two scenarios. Often, one might like to examine a larger number of options. For example, if current fishing mortality exceeds F_{max}, then one could explore various ways to reduce fishing mortality in gradual steps as well as exploring the consequences of various types of "status quo" options. The simulation approach is versatile enough to handle fixed catch, fishing mortality, and biomass objectives, as well as objectives involving relative change. Thus, one could have any of the following objectives for fishing mortality: achieve $F = 0.40$/yr, achieve $F = F_{0.1}$, reduce F by 40%, or adjust F so that biomass changes a given fixed or relative amount.

In some fisheries, catch and population projections may be highly dependent on the assumptions made about recruitment. When this is the case, it may be helpful to quantify the uncertainty separately for various segments of the population. For example, we computed the distribution of relative change in age 3+ biomass of cod (from 1989 to 1991) for various choices of the TAC. The wide confidence bands (Fig. 3) reflect the large uncertainty in future recruitment. We could have quantified the relative change in the biomass of age 5+ fish. From the ADAPT run based on 1989 data, we already have an estimate of age-3 biomass in 1989. This biomass can be projected forward to age 5 in 1991; hence, we do not need to generate a random value for recruitment. The uncertainty in the biomass of age 5+ fish should thus be smaller than the uncertainty in age 3+ biomass. Unfortunately, the latter quantity may be of greater interest.

Conclusions

Monte Carlo simulation has long been regarded as a very useful quantitative tool, especially for sensitivity analysis (e.g., Pope and Gray 1983, Rivard 1983). It is also quite useful for studying the properties of specific assessment procedures (e.g., Mohn 1983, Kimura 1989). Here, we follow Francis (1991) and use it to quantify the risks of not meeting the objectives

for the fishery as a function of the management measures imposed. The simulation approach we present can be used with assessment models other than ADAPT. For example, one could use Monte Carlo simulation to quantify the effects of uncertainty in input data, assumptions, and model formulation on the outputs from the CAGEAN (Deriso et al. 1985) or stock synthesis (Methot 1990) methods. We believe that this simulation framework is not only a versatile and intuitive method to estimate uncertainty, risks, and costs, but in many cases it may also be the only practical way to incorporate some types of input uncertainty which are not estimated statistically. Because the estimated uncertainties in the model outputs are conditional on what is known and what is assumed about the inputs, failure to acknowledge possible sources of uncertainty in a realistic manner may lead to overly optimistic views of the uncertainties in the model outputs. The Monte Carlo approach forces one to examine the nature and magnitudes of the uncertainties in the inputs and in the model formulation, and it allows one to study how uncertainties are propagated through the assessment and into the projections ultimately used for management recommendations.

It appears feasible to quantify risks and costs for a wide variety of management options when the assessments are accomplished by any of a variety of analytical models. It remains to determine what risks (and costs) should be quantified, how much risk is acceptable, and for how long. For example, we do not know how to quantify the risk of stock collapse due to recruitment failure, but we might wish to quantify the risk of the spawning biomass falling below 20% of the virgin level in three years out of five. If we assume that this represents a dangerous situation (see Beddington and Cooke 1983, Brown 1990, and Goodyear 1990, for thoughtful discussions), then the risk should be kept low. On the other hand, if we consider the risk of exceeding the economically-optimal fishing mortality (however defined), then we might like the risk to be close to 50%, i.e., as likely to be above the optimum as below it. (Of course, we should consider the relative costs of over- and undershooting the target mortality). If F is not close to the economic optimum fishing mortality, then one must also devise a way to determine what is the best trajectory to take for arriving at the long-term goal. It is beyond the scope of this paper to address what are appropriate goals, biological reference points, and trajectories.

Finally, for any stock assessment, the results of a Monte Carlo simulation study are necessarily conditional on what is assumed about the sources of uncertainty, including the model chosen for the assessment. Since decisions about some of the sources of uncertainty are subjective, the results are personal views of uncertainty, risk, cost, etc. If three scientists assess a given stock, they can generate three separate sets of simulation outputs. The combination of their simulations provides a picture of their collective uncertainty about the assessment results. Alternatively, they can agree that a minimal estimate of the uncertainty is provided by the one set of results that are the least uncertain.

A more detailed study of the relative sensitivities of the assessment outputs and risk curves to the choice of input distributions can be carried out via sensitivity analysis (Miller 1974). In this Monte Carlo framework, sensitivity analysis would consist of introducing planned perturbations to the input-uncertainty distributions and then measuring the overall effect on the model's outputs. This should aid in the identification of key inputs so that more effort could be placed on improving their estimates. This is more difficult than it may seem. A given input that is perturbed during the sensitivity analysis (say, catch at age) will cause different degrees of change in the various output distributions: stock sizes, fishing mortalities, $F_{0.1}$, projected catches, etc. Furthermore, this impact may change over time. For instance, assumptions about recruitment become very dominant as the projections are made further ahead in time. Nonetheless, sensitivity analysis can be very useful in identifying trade-offs between the benefits of precision and the cost of obtaining that precision.

Acknowledgments

Partial support for this study was provided through the Cooperative Institute for Marine and Atmospheric Studies by National Oceanic and Atmospheric Administration (NOAA) Cooperative Agreement NA90-RAH-0075 and by the Canadian Government's Atlantic Fisheries Adjustment Program (Northern Cod Science Program). We thank Nicholas Payton for programming assistance and Peter Shelton, Al Pinhorn, Donald Parsons, and two anonymous reviewers for helpful comments.

Citations

Baird, J.W., C.A. Bishop, and W.B. Brodie
1990 The assessment of the cod stock in NAFO Divisions 2J, 3K and 3L. CAFSAC (Can. Atl. Fish. Sci. Adv. Comm.) Res. Doc. 90/18.

Beddington, J.R., and J.G. Cooke
1983 The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 50 p.

Bergh, M.O., and D.S. Butterworth
1987 Towards rational harvesting of the South African anchovy considering survey imprecision and recruitment variability. S. Afr. J. Mar. Sci. 5:937–951.

Brown, B.
1990 Use of spawning stock size considerations in providing fishery management advice in the North Atlantic—a brief review. ICCAT (Int. Comm. Conserv. Atl. Tunas) Collect. Vol. Sci. Pap. 32(2):498–506.

Canada Department of Fisheries and Oceans
1991 1991 Atlantic groundfish management plan 1990. Ottawa, 114 p.

Conser, R.J., and J.E. Powers
1990 Extensions of the ADAPT tuning method designed to facilitate assessment work on tuna and swordfish stocks. ICCAT Collect. Vol. Sci. Pap. 32: 461–467.

Deriso, R.B., T.J. Quinn II, and P.R. Neal
1985 Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815–824.

Efron, B.
1982 The jackknife, the bootstrap and other resampling plans. Soc. Ind. Appl. Math, Philadelphia.

Francis, R.I.C.C.
1991 Risk analysis in fishery management. Northwest Atl. Fish. Organ. Sci. Counc. Stud. 16:143–148.

Gavaris, S.
1980 Use of a multiplicative model to estimate catch rate and effort from commercial data. Can. J. Fish. Aquat. Sci. 37: 2272–2275.
1988 An adaptive framework for the estimation of population size. CAFSAC (Can. Atl. Fish. Sci. Adv. Comm.) Res. Doc. 88/29.

Gavaris, S., and C.A. Gavaris
1983 Estimation of catch at age and its variance for groundfish stocks in the Newfoundland region. Can. Spec. Publ. Fish. Aquat. Sci. 66:178–182.

Goodyear, C.P.
1990 Spawning stock biomass per recruit: The biological basis for a fisheries management tool. ICCAT Collect. Vol. Sci. Pap. 32:487–497.

Gulland, J.A., and L.K. Boerema
1973 Scientific advice on catch levels. Fish. Bull., U.S. 71: 325–335.

ICCAT (International Commission for the Conservation of Atlantic Tunas)
1990 Appendix 10 to Annex 8. *In* Report for biennial period, 1988–89, Part II (1989). Madrid, Spain [Engl. version].

Kendall, M., and A. Stuart
1977 The advanced theory of statistics, vol. 1, 4th ed. Macmillan, NY.

Kimura, D.K.
1989 Variability, tuning, and simulation for the Doubleday-Deriso catch-at-age model. Can. J. Fish. Aquat. Sci. 46: 941–949.

Methot, R.D.
1990 Synthesis model: An adaptable framework for analysis of diverse stock assessment data. Int. N. Pac. Fish. Comm. Bull. 50:259–277.

Miller, D.R.
1974 Sensitivity analysis and validation of simulation models. J. Theor. Biol. 48:345–360.

Mohn, R.K.
1983 Effects of error in catch and effort data on tuning cohort analysis, with a postscript on logistic production models. Can. Spec. Publ. Fish. Aquat. Sci. 66:141–150.

Parrack, M.L.
1986 A method of analyzing catches and abundance indices from a fishery. ICCAT (Int. Comm. Conserv. Atl. Tunas) Collect. Vol. Sci. Pap. 24:209–221.

Pelletier, D., and A. Laurec
1990 Toward more efficient adaptive TAC policies with error-prone data. Northwest Atl. Fish. Organ. SCR Doc. 90/100 (ser. N1835).

Pope, J.G.
1972 An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. Northwest Atl. Fish. Res. Bull. 9:65–74.
1983 Analogies to the status quo TACs: Their nature and variance. Can. Spec. Publ. Fish. Aquat. Sci. 66:99–113.

Pope, J.G., and D.J. Garrod
1975 Sources of error in catch and effort quota regulations with particular reference to variations in the catchability coefficient. Int. Comm. Northwest Atl. Fish. Res. Bull. 11:17–30.

Pope, J.G, and D. Gray
1983 An investigation of the relationship between the precision of assessment data and the precision of total allowable catches. Can. Spec. Publ. Fish. Aquat. Sci. 66:151–157.

Pope, J.G., and J.G. Shepherd
1982 A simple method for the consistent interpretation of catch-at-age data. J. Cons. Cons. Int. Explor. Mer 40:176–184.

Powers, J.E., and V.R. Restrepo
1992 Additional options for age-sequenced analysis. ICCAT (Int. Comm. Conserv. Atl. Tunas) Collect. Vol. Sci. Pap. 39: 540–553.

Prager, M.H., and A. MacCall
1988 Sensitivities and variances of virtual population analysis as applied to the mackerel, *Scomber japonicus*. Can. J. Fish. Aquat. Sci. 45:539–547.

Restrepo, V.R., and W.W. Fox Jr.
1988 Parameter uncertainty and simple yield-per-recruit analysis. Trans. Am. Fish. Soc. 117:282–289.

Rivard, D.
1983 Effects of systematic, analytical, and sampling errors on catch estimates: A sensitivity analysis. Can. Spec. Publ. Fish. Aquat. Sci. 66:114–129.

Saila, S.B., E. Lorda, and H.A. Walker
1985 The analysis of parameter error propagation in simple fishery models. Mar. Res. Econ. 1(3):235–246.

Sampson, D.B.
1987 Variance estimators for virtual population analysis. J. Cons. Cons. Int. Explor. Mer 43:149–158.

Seber, G.A.F., and C.J. Wild
1989 Nonlinear regression. John Wiley, NY.

Behavior of individually-identified sei whales *Balaenoptera borealis* during an episodic influx into the southern Gulf of Maine in 1986

Mark R. Schilling
Cetacean Research Unit, P.O. Box 159, Gloucester, Massachusetts 01930

Irene Seipt
Cetacean Research Program, Center for Coastal Studies
Provincetown, Massachusetts 02657

Mason T. Weinrich*
Cetacean Research Unit, P.O. Box 159, Gloucester, Massachusetts 01930

Steven E. Frohock
Atlantic Cetacean Research Center, P.O. Box 1413, Gloucester, Massachusetts 01930

Anne E. Kuhlberg
Cetacean Research Unit, P.O. Box 159, Gloucester, Massachusetts 01930

Phillip J. Clapham
Cetacean Research Program, Center for Coastal Studies
Provincetown, Massachusetts 02657
Department of Zoology, University of Aberdeen, Aberdeen AB9 2TN, Scotland

Abstract.– Sei whales *Balenoptera borealis* are noted for major fluctuations in distribution, often in response to local availability of prey. An influx of sei whales occurred in the southern Gulf of Maine during summer 1986. Forty-seven individuals (including four mothers with calves) were photographically identified using natural markings, including dorsal-fin notches, placement of small circular scars on the animal's flank, and natural variation in dorsal-fin shape and pigment swaths along the dorsal surface behind the blowholes. Seventeen of these whales (36.1%) were photographed on more than one day, and the period between first and last sighting of individuals ranged from one to 66 days. Only six animals were sighted in more than one region in the southern Gulf of Maine. Observed behavior included traveling, nearsurface skim feeding, lunge feeding, and (rarely) "milling" or breaching. Group sizes were small and variable. Two individuals were matched to photographs taken in other regions in or near offshore Gulf of Maine waters. We hypothesize that the southern Gulf of Maine represents a short-term feeding site. The occurrence of individuals without sufficient marks for individual recognition suggests that photoidentification is of limited value in the study of this species.

Manuscript accepted 5 July 1992.
Fishery Bulletin, U.S. 90:749–755 (1992).

Most species of baleen whales undertake seasonal migrations between high-latitude feeding grounds and warmer breeding areas (Kellogg 1929, Slijper 1962, Mackintosh 1965). Populations often show annual variations in local spatial distribution within these areas (Wursig et al. 1985). While the factors causing these variations are not well defined for breeding grounds, it has been suggested that they are explained on feeding grounds by differences in prey distribution (Whitehead and Carscadden 1988, Payne et al. 1990). Because of the energetic demands upon large whales (Lockyer 1981) and the unpredictable distribution of their prey, such areal variation would be expected if the animals were seeking to maximize their feeding efficiency.

Sei whales *Balaenoptera borealis* have been reported to have greater variation in distribution on their feeding grounds than most baleen whale species (Horwood 1987). Sei whales have been reported in considerable numbers for brief periods outside of their regular range in Norway (1885, 1898, and 1919), Finland (1885), and Scotland (1906) (Tomilin 1957, Jonsgard and Darling 1977). Ingebrigtsen (1929) reported large annual changes in distribution off the Faroe Islands. These changes are hypothesized to be related to local increases in planktonic productivity (International Whaling Commission 1977, Horwood 1987).

Sei whales off the northeastern United States and southeastern Canada have been little studied. Mitchell and Chapman (1977) hypothesized

* Author to whom reprint requests should be sent.

the existence of a "stock" of sei whales centered around Nova Scotia. During the spring these animals are thought to occur on the southern edge of George's Bank (Mitchell and Chapman 1977, CETAP 1982). During June and July, they move north to the southern Scotian Shelf, then onto Brown's, Bacarro, and Roseway Bank from August to October (Sutcliffe and Brodie 1977). The lack of sightings in these areas, plus late-winter/early-spring strandings in South Carolina, Louisiana, and Mississippi suggest a southward movement after October (Mead 1977). The inshore waters of the southern Gulf of Maine are rarely used by sei whales (CETAP 1982, Payne et al. 1990).

In this paper, we report on the photoidentification, occupancy patterns, surface behavior, and social behavior of individual sei whales found in the Gulf of Maine during an unexpected summer influx of this species in 1986, documented through daily shipboard surveys. We also report results of photographic identification of individual sei whales, and evaluate the feasibility of such techniques for investigations of this species.

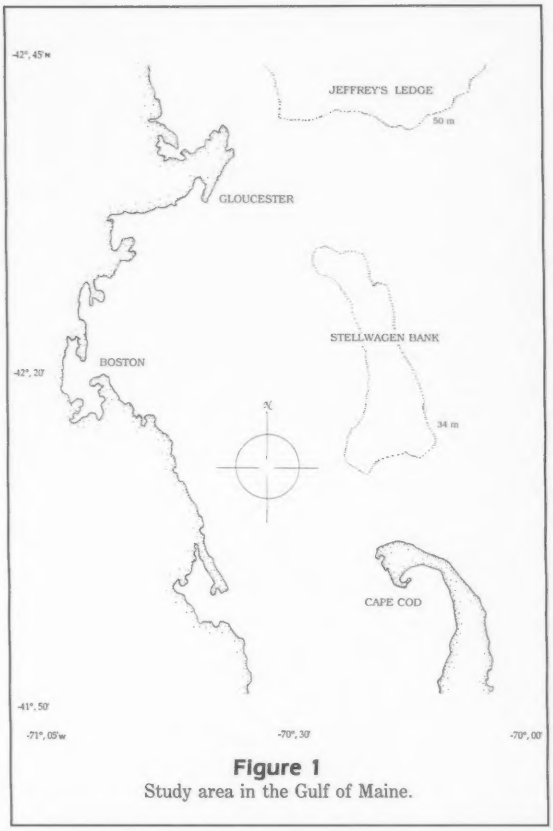


Figure 1
Study area in the Gulf of Maine.

Methods

Non-systematic surveys of the southern Gulf of Maine were conducted daily (weather permitting) from mid-April through October on commercial whale-watching and research vessels operating out of Provincetown and Gloucester, Massachusetts during 1980–91. In 1986, the only year of sei whale abundance, the number of vessels collecting data varied. There were usually six to nine 4-hr cruises daily from each port. Vessels were 18–30 m long diesel-powered whale-watching vessels and 6.7–14 m long research vessels powered by sail, diesel, or outboard engines. Whale-watch cruises were typically 4–5 hr in duration, while research-vessel cruises often lasted from dawn until dusk.

Search effort by whale-watching vessels was concentrated on the southern and northern edges of Stellwagen Bank and the southern edge of Jeffrey's Ledge because of the concentrations of whales there (Fig. 1). Stellwagen Bank is a shallow glacial deposit with a sand substrate, at 20–40 m. Southern Jeffrey's Ledge has a mean depth of 48 m, and is a mixture of sand, gravel, and rocks. Depths surrounding both areas extend to 182 m. In both areas there is upwelling, caused by steep topography which enriches the biological productivity of the area, providing food for whales (Kenney and Winn 1986).

For each sighting data included location, direction and speed of animal movement (based on LORAN-C readings taken every 5–10 min), environmental conditions, behavioral information including respiration intervals (to the nearest second) of individuals recognizable by natural marks, notable non-respiratory surface behavior, and associations among whales. Two or more whales were considered associated if they were in close proximity and consistently coordinated in the timing and direction of their surfacings.

Cow/calf pairs were treated as single animals for an analysis of occupancy periods (the time between first and last sighting), assuming that the calf's movements are determined by those of its mother. Calves were designated based on the animal being considerably smaller than any other animals, and on the continuous association between two individuals for at least 30 min or on more than one day. Personnel were experienced in observing mother-calf pairs of humpback *Megaptera novaeangliae* and fin *Balaenoptera physalus* whales. To determine mean associated group size, mother and calf pairs were counted as two individuals.

Fecal samples were scooped from the surface in a 5-gallon bucket on two days in August 1986 near northern Stellwagen Bank. The material was frozen until

examination. Prey remains were identified to species by staff of Allied Whale at the College of the Atlantic, Bar Harbor, Maine.

High-speed (ISO 400) black-and-white film was used in 35 mm single-lens reflex cameras equipped with telephoto lenses (range 200–400 mm) to photograph whales. When possible, three regions were photographed on each side of a whale: between the tip of the snout and the blowhole, the flank between the blowhole and dorsal fin, and the dorsal fin.

Photos were classified as matchable or unmatchable based on the same criteria defined by Seipt et al. (1990) for fin whale photoidentification. Unmatchable photos had poor focus, were not perpendicular to the whale, or were too far from the whale to distinguish marks clearly (generally photos taken at distances >100 m from the whale). For photos judged matchable, a whale was classified as a unique individual based on the presence of one or more of the following characters: recognizable scars, a distinctive dorsal-fin shape (including dorsal-fin notches), or detectable pigmentation on the flank between the blowhole and dorsal fin. If at least one of these features was not present in a photograph, it was discounted.

Matches of individual whales were made within independent photographic collections of the Atlantic Cetacean Research Center (Gloucester MA), the Center for Coastal Studies (Provincetown MA), and the Cetacean Research Unit (Gloucester MA) by personnel experienced in photo-identifying individual humpback or fin whales. The independent catalogs of identified whales from each organization were compared, with matches being confirmed by both other groups, resulting in a single collective catalog of identified whales. Only matches agreed upon by all parties were accepted.

In order to examine long-range movements of sei whales, photographs were solicited from researchers working in the Gulf of Maine for comparison with the unified catalog described above. Each set of photographs obtained in different geographic areas or years were treated separately.

Data for this study were stored on PC-based microcomputers and statistical analyses were performed using SPSS (1989) statistical software package for PC's, including calculation of mean values and standard deviations. A two-tailed t-test was used to compare mean values for associated group sizes between different parts of the study area, and a χ^2 test was used to test potential differences in group sizes when a mother-calf pair was present in the group (Zar 1984).

Results

Photoidentification

A total of 240 sei whale sightings took place between 29 June and 20 September 1986. Photographs were taken on 182 sightings (75.8%). In 51 photographed sightings (28.0% of all photographed sightings) the animal could not be reliably identified because of poor photographic quality.

Photoidentification of some individual sei whales was possible using variation in dorsal-fin shape, placement of small circular scars on either flank, and light pigment swaths behind the dorsal fin (Fig. 2). A total of 47 identifiable non-calf sei whales and 4 calves were photographed; of these, 19 were identifiable based on notches in their dorsal fin alone, 4 based on the locations of small circular scars on the flanks, and 10 based on both distinctive dorsal fins and circular scars. No attempt was made to photoidentify calves. Twelve whales were identified based on dorsal-fin shape and pigment swaths behind the blowhole. One sei whale was missing its dorsal fin, and one had a large white scar visible on the lower portion of its right caudal peduncle. In 12 cases, animals did not have distinctive marks by which they could be identified reliably.

Occurrence and occupancy

The 47 individual sei whales were sighted on as few as 1 and as many as 15 separate days ($\bar{x}$ 2.4, SD 3.0) (Fig. 3). Seventeen individuals (36.2%) were observed on more than one day; the mean period for resighted animals between first and last sighting was 26.8 days (SD 24.1, median 20.0). No individual sighting record spanned more than 66 days from first to last sighting.

Twenty-six individuals (55.3%) were initially photographed on southern Stellwagen Bank, 15 (31.9%) on northern Stellwagen Bank, 4 (8.5%) on Jeffrey's Ledge, 1 (2.1%) in Massachusetts Bay (west of Stellwagen Bank), and 1 (2.1%) in the Great South Channel. Only 6 animals out of the 17 resighted were photographed in more than one of these areas. Of these, four were first seen on southern Stellwagen and subsequently moved north on the Bank; one animal showed the reverse pattern. The remaining one was first photographed on southern Jeffrey's Ledge and later resighted on northern Stellwagen Bank. One of these whales moved between northern and southern Stellwagen Bank at least five times; this individual also had the greatest number of sightings (15) and the longest period between first and last sighting.

Behavior and movement patterns

A total of 752 respiration intervals were recorded during 53 sei whale sightings (from at least 15 different individuals). Inter-respiration intervals showed a range of 2–928 sec, with a mean of 60.8 sec (SD 78.0 sec). The most common respiratory pattern was a single breath followed by a short dive of 45–90 sec. On only four sightings did the whales submerge for prolonged dives of 6–11 min, and they did so repeatedly within the observation.

The regular breath intervals and lack of prolonged dives often appeared associated with near-surface feeding. In the most common feeding behavior, sei whales would take a breath and then roll 45–90° around their longitudinal axis while ~3 m below the surface. The mouth was often slightly open as the animal swam forward. There were four observations of lunge feeding, when the whale rapidly surfaced with its mouth opened. During lunges, no rolling was observed. On one of four occasions of lunging, the same individual alternated lunges with the more common nearsurface feeding behavior.

During feeding and swimming, the whales often remained in an area of ~0.5 km^2 for over an hour. Whales would either change swimming direction with each breath, or travel in a straight line for 10 min or less before reversing, resulting in minimal net movement at the surface.

Figure 2
Photographic match of sei whale *Balaenoptera borealis* #22, utilizing both circular scars and dorsal-fin notches as aids in identification. Note the pattern of circular scars below the dorsal fin, particularly the large circular scar below and immediately posterior to the dorsal fin, and the slightly blunted tip of the fin itself. Top photograph was taken 10 August 1986, bottom photograph on 22 August 1986.

Defecations were observed nine times. Feces were bright red and contained chunks of particulate matter. Only mandibles from the copepod *Calanus finmarchicus* were subsequently identified in fecal material.

While feeding and traveling comprised most of the behavioral events (both time and number), milling (at least three socializing with one another while moving in apparently random directions, rolling, and remaining on the surface continually for over 10 min) was seen four times. This was always associated with one whale leaving the group either during or immediately after the milling period. Breaching was seen once, when a single animal breached twice in rapid succession.

Social behavior

Sei whales were seen in groups of 1—6 individuals. Mean group size was 1.8, and was the same on both

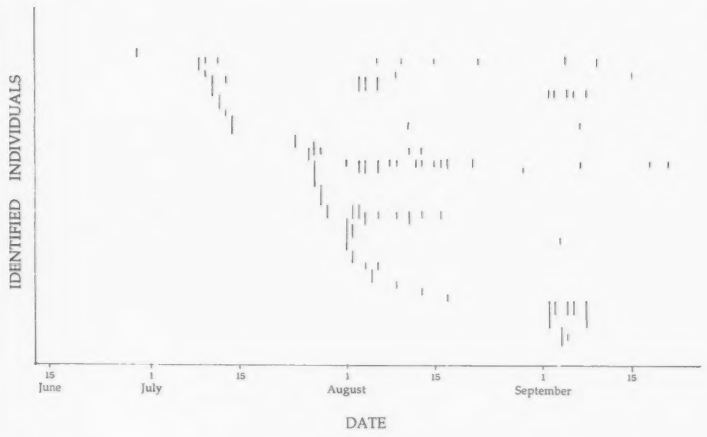


Figure 3

Occurrence of individual sei whales *Balaenoptera borealis* in the southern Gulf of Maine during 1986. Individual whales are ordered (top to bottom) by date of first sighting; each row of marks represents the dates on which one individual was seen during the year. Vertical marks represent single whales.

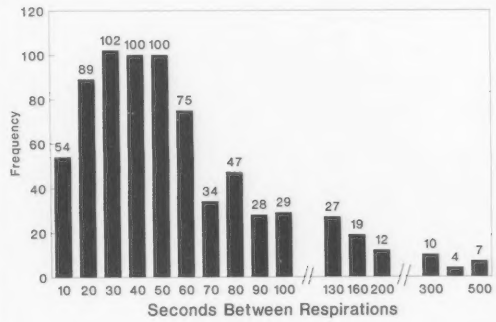


Figure 4

Histogram showing the distribution of breath intervals (sec) from sei whales *Balaenoptera borealis* recorded during 52 sightings in the 1986 season on northern Stellwagen Bank. Note the scale change for the longer breath intervals due to their infrequent occurrence.

northern and southern Stellwagen Banks, where most observations took place (two-tailed t-test, p 0.93, 1 df). Resightings of individual animals on successive days were recorded 14 times. In cases where all members of an associated group were photoidentified, only one pair of animals was seen together on two days; one whale from this pair was later sighted with a different associate two days later. These data indicate that individual associations were transient, generally lasting less than 24 hr.

Of 13 cow/calf pairs, 3 (23.0%) were associated with 1 or more other whales, while 48 (51.6%) of the 93 non-calf groups involved 2 or more whales. Frequency of association with another whale was not statistically significant between groups with and without mother-calf pairs (χ^2 3.7, p 0.06, 1 df). Cow/calf pairs were never seen with more than one associate.

Comparisons with other data sets

Sei whales identified in the southern Gulf of Maine in 1986 were compared with one 1984 photograph from Georges Bank (Atlantic Cetacean Research Center), one from Stellwagen Bank in 1987 (Plymouth Marine Mammal Center), one from Jeffrey's Ledge in 1988 (Cetacean Research Unit), three from the Scotian Shelf in 1988 (Atlantic Cetacean Research Center and Nancy Miller), and four from the Scotian Shelf in 1989 (New England Aquarium). There were two matches. Sei whale 33 was photographed on 11 June 1984 between Wilker's and Oceanographer's Canyon on the southern edge of Georges Bank (40°05′N, 68°19′W), 176 nmi from the 1986 sighting; sei whale 19 was photographed on 28 August 1989 on the Nova Scotian Shelf (42°57′N, 65°09′W), 211 nmi from its 1986 sighting.

Discussion

Photoidentification of individual animals has been accomplished for numerous baleen and toothed whales (Katona et al. 1980, Dorsey 1983, Agler et al. 1990, Seipt et al. 1990). Our results indicate that some sei whales can be identified using variations in natural markings. Dorsal-fin shape, natural pigment patterns, and scarring were all useful features. The presence of circular scars along the flank—hypothesized to be caused by small sharks (Shevchenko 1977), lampreys, or pathogenic microorganisms (Tomilin 1957, Rice 1977)—and dorsal-fin notches (unknown origin) both facilitated identification of the individuals. While these techniques work within a single season, the possibility of acquiring new dorsal-fin notches, new scars, or

having scars change with age (Shevchenko 1977) might make identification over a prolonged period difficult.

The lack of distinctive markings on some individuals indicates that while photoidentification is useful in studies of sei whales, it is not likely to allow identification of all members of the population. Because we were unable to determine the sex and/or age of the animals involved, it is impossible to indicate whether distinctive markings were related to age or sex.

The photographic matches of sei whales in the southern Gulf of Maine to both Georges Bank and the Scotian Shelf lend some support to the idea that whales in the 1986 influx were from the closest-known geographic stock. However, given the dearth of knowledge concerning the biogeography of this species, and Brown's (1977) record of a sei whale moving 4000 km in 10 days, many or all of the animals reported here may come from other locations in the North Atlantic. During the year of the southern Gulf of Maine influx, abnormally high levels of *Calanus finmarchicus* were present on Stellwagen Bank (Payne et al. 1990). Our findings therefore lend support to the hypothesis that sei whales show annual areal fluctuations to take maximal advantage of changes in local productivity throughout their range. Whether each individual independently found the increased copepod productivity, or whether social factors were involved in the influx, remains an open question which our data do not address.

Most of the sei whales in 1986 were seen during late July and early August, with a secondary peak in early September (Fig. 3). This suggests that the local productivity provided a brief stop-over point during the summer feeding season. Repeated resightings of a few individuals during the study suggest that a small number of animals found prey levels adequate to allow a prolonged occupancy period.

Observed behavior of sei whales was similar to that previously described (Tomilin 1957, International Whaling Commission 1977, Horwood 1987). The relatively small variation around the mean breath interval shows a departure from the standard balaenopterid pattern of hyperventilation, e.g., several breaths taken in rapid succession followed by a longer diving period (Gunther 1949, Leatherwood et al. 1976). The rolling we observed during apparent feeding behavior differs from that described by Tomilin (1957) who did not observe this species roll during feeding.

Social groups observed in this study are similar to those reported by studies of other balaenopterids, with individuals being sighted either alone or in small groups (Nemoto 1964, Dorsey 1983, Whitehead and Carlson 1988). Lockyer (1977) reported a mean associated group size of 2.4, slightly higher than the 1.8 reported here. Since she did not define an associated group, however, direct comparisons are difficult. Further, if there is a correlation between the associated group-size and prey patch-size (such as that described for humpback whales by Whitehead 1983), it is possible that the larger group size observed could be explained by the more productive Antarctic waters. Our limited data also suggest that, as in other baleen whales, cow/calf pairs were more solitary than other animals, both in frequency of association with other individuals and in overall group size. This has previously been documented in humpback whales (Clapham and Mayo 1987), gray whales *Eschrichtius robustus* (Swartz 1986), and right whales *Eubalaena australis* (Payne 1986).

Acknowledgments

Many people helped gather field data including Cindy Belt, Carole Carlson, Peggy Christian, Lisa Frohock, David Mattila, Sharon Pittman, and many interns. Polly Hamlin (CCS), Maribel Marcy (CRU), and Lisa Frohock (ACRC) helped considerably in compiling raw data. Scott Kraus (New England Aquarium), Nancy Miller, Fred Wenzel, and Dave Wiley all provided photographs of sei whales for comparison with our 1986 sightings. Dr. Steven Katona and his colleagues at the College of the Atlantic generously took their time to examine the fecal material. We thank the owners and crews of the Dolphin Fleet, Cape Ann Whale Watch, Cap't Bill and Sons Whale Watch, and Gloucester Whale Watch for their logistical help and support. Funding for this study came from the National Marine Fisheries Service, the American Cetacean Society/Los Angeles Chapter, the Essex County Ecology Center, and Gloucester Whale Watch: we are indebted to them all.

Citations

Agler, B.A., J.A. Beard, R.S. Bowman, H.D. Corbett, S.E. Frohock, M.P. Hawvermale, S.E. Katona, S.S. Sadove, and I.E. Seipt
1990 Finback whale, *Balaenoptera physalus*, photographic identification: Methodology and preliminary results from the western North Atlantic. Rep. Int. Whaling Comm. (Spec. Issue 12):349–356.

Brown, S.G.
1977 Some results of sei whale marking in the Southern Hemisphere. Rep. Int. Whaling Comm. (Spec. Issue 1):39–43.

CETAP (Cetacean and Turtle Assessment Program)
1982 A characterization of marine mammals and turtles in the mid- and north Atlantic areas of the U.S. outer continental shelf. Final Report of the Cetacean and Turtle Assessment Program, University of Rhode Island, to the Bureau of Land Management, Washington D.C. Kingston, 450 p.

Clapham, P.J., and C.A. Mayo
1987 Reproduction and recruitment of individually identified humpback whales, *Megaptera novaeangliae*, observed in Massachusetts Bay, 1979–1985. Can. J. Zool. 65:2853–2863.

Dorsey, E.M.
1983 Exclusive adjoining ranges in individually identified minke whales in Washington state. Can. J. Zool. 61:174–181.

Gunther, E.R.
1949 Habits of the fin whale. Discovery Rep. 25:113–142.

Hammond, P.S., S.A. Mizroch, and G.P. Donovan (editors)
1990 Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Rep. Int. Whaling Comm. (Spec. Issue 12), 440 p.

Horwood, J.W.
1987 The sei whale: Population biology, ecology, and management. Croom Helm Ltd., Kent, England, 375 p.

Ingebrigtsen, A.
1929 Whales caught in the North Atlantic and other seas. Int. Counc. Explor. Sea, Rapp. P.V. Reun. 56:1–26.

International Whaling Commission
1977 Report of the special meeting of the scientific committee on sei and Bryde's whales. Rep. Int. Whaling Comm. (Spec. Issue 1):1–9.

Jonsgard, A., and K. Darling
1977 On the biology of the eastern North Atlantic sei whale. Rep. Int. Whaling Comm. (Spec. Issue 1):124–129.

Katona, S.K., P. Harcourt, J.S. Perkins, and S.D. Kraus
1980 Humpback whales: A catalog of individuals identified by fluke photographs. College of the Atlantic, Bar Harbor, ME, 169 p.

Kellogg, R.
1929 What is known of the migration of some of the whalebone whales. Smithson. Inst. Annu. Rep., 1928, Publ. 2981, p. 467–494.

Kenny, R.D., and H.E. Winn
1986 Cetacean high-use habitats of the northeast United States continental shelf. Fish. Bull., U.S. 84:345–357.

Leatherwood, S., D.C. Caldwell, and H.E. Winn
1976 Whales, dolphins and porpoises of the western North Atlantic: A guide to their identification. NOAA Tech. Rep. NMFS CIRC-396, 176 p.

Lockyer, C.
1977 Some possible factors affecting age distribution of the catch of sei whales in the Antarctic. Rep. Int. Whaling Comm. (Spec. Issue 1):63–70.
1981 Growth and energy budgets of large baleen whales from the southern hemisphere. *In* FAO Advisory Committee on Marine Resources Research, Working Party on Marine Mammals (ed.), Mammals in the seas: Vol. 3. Large cetaceans, p. 379–487. FAO, Rome, 504 p.

Mackintosh, N.A.
1965 The stocks of whales. Fishing News (Books), Ltd., London, 232 p.

Mead, J.
1977 Records of sei and Bryde's whales from the Atlantic coast of the United States, the Gulf of Mexico, and the Caribbean. Rep. Int. Whaling Comm. (Spec. Issue 1):113–116.

Mitchell, E.A., and D.G. Chapman
1977 Preliminary assessment of stocks of the Northwest Atlantic sei whales. Rep. Int. Whaling Comm. (Spec. Issue 1): 117–120.

Nemoto, T.
1964 Schools of baleen whales in the feeding areas. Sci. Rep. Whales Res. Inst. 18:89–110.

Payne, P.N., D. Wiley, S. Young, S. Pittman, P.J. Clapham, and J. Jossi
1990 Recent fluctuations in the abundance of baleen whales in the southern Gulf of Maine in relation to changes in prey abundance. Fish. Bull., U.S. 88:687–696.

Payne, R.
1986 Long term behavioral studies of the southern right whale (*Eubalaena australis*). Rep. Int. Whaling Comm. (Spec. Issue 10):161–167.

Rice, D.W.
1977 Synopsis of biological data on the sei whale and Bryde's whale in the Eastern North Pacific. Rep. Int. Whaling Comm. (Spec. Issue 1):92–97.

Seipt, I.E., P.J. Clapham, C.A. Mayo, and M.P. Hawvermale
1990 Population characteristics of individually identified fin whales *Balaenoptera physalus* in Massachusetts Bay. Fish. Bull., U.S. 88:271–277.

Shevchenko, V.I.
1977 Application of white scars to the study of the location and migrations of sei whale populations in Area III of the Antarctic. Rep. Int. Whaling Comm. (Spec. Issue 1):130–134.

Slijper, E.J.
1962 Whales. Basic Books, NY, 475 p.

SPSS
1989 Statistical package for the social sciences (PC+3.1). SPSS, Inc., Chicago.

Sutcliffe, W.H. Jr., and P.F. Brodie
1977 Whale distribution in Nova Scotia waters. Fish. Mar. Serv. Tech. Rep. 22, Fisheries and Environment Canada, 22 p.

Swartz, S.L.
1986 Gray whale migratory, social, and breeding behavior. Rep. Int. Whaling Comm. (Spec. Issue 8):207–229.

Tomilin, A.G.
1957 Mammals of the U.S.S.R. and adjacent countries. Vol. 9, Cetacea. Akad. Nauk SSSR, Moscow, 756 p. [in Russ.]. (Trans. by the Israel Prog. Sci. Transl., Jerusalem, 1967, 717 p.; avail. NTIS, Springfield VA, as TT-65-50086.)

Whitehead, H.
1983 Structure and stability of humpback whale groups off Newfoundland. Can. J. Zool. 61:1391–1397.

Whitehead, H., and C. Carlson
1988 Social behavior of feeding finback whales off Newfoundland: Comparisons with the sympatric humpback whale. Can. J. Zool. 66:217–221.

Whitehead, H., and J.E. Carscadden
1985 Predicting inshore whale abundance—Whales and capelin off the Newfoundland coast. Can. J. Fish. Aquat. Sci. 42: 976–981.

Wursig, B., E.M. Dorsey, M.A. Fraker, R.S. Payne, and W.J. Richardson
1985 Behavior of bowhead whales *Balaena mysticetus* summering in the Beaufort Sea: A description. Fish. Bull., U.S. 83: 357–377.

Zar, J.H.
1984 Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, 718 p.

Population dynamics of pelagic armorhead *Pseudopentaceros wheeleri* on Southeast Hancock Seamount

David A. Somerton

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396
Present address: Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Seattle, Washington 98115-0070

Bert S. Kikkawa

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396

Abstract.–Pelagic armorhead *Pseudopentaceros wheeleri* are the target of a directed trawl fishery on many of the southern Emperor–northern Hawaiian Ridge seamounts. The population dynamics of armorhead for the period 1970–90 were reconstructed for Southeast Hancock seamount, the southernmost of the seamounts commercially fished, by using commercial catch-and-effort statistics, various biological measurements, and research stock-survey data. The population declined almost continuously from a 1972 high of 5500 metric tons (t) to a 1989 low of 25 t. In addition to the intense fishery, this decline was due partly to the sporadic pattern of armorhead recruitment. Natural mortality rate was estimated as 0.54/year; however, females had a higher mortality rate than males.

Pelagic armorhead *Pseudopentaceros wheeleri* have an unusual life history that includes two distinct postlarval phases: a pelagic juvenile phase, and a demersal adult phase. During the first 1.5–2.5 years of their lives (Uchiyama and Sampaga 1990), juvenile armorhead inhabit the epipelagic zone over a broad area of the northeast Pacific, where they acquire large fat reserves before migrating westward to the southern Emperor–northern Hawaiian Ridge (SE–NHR) seamounts (Boehlert and Sasaki 1988, Humphreys et al. 1989). After arriving at the seamounts, armorhead mature and assume demersal habits. Because of the rigors of spawning or the inability to obtain sufficient prey (Seki and Somerton, In prep.), adult armorhead subsequently lose weight to such an extent that they eventually become emaciated and moribund (Humphreys et al. 1989).

Armorhead form dense nighttime aggregations over the relatively flat summits of the SE–NHR seamounts. Soon after these aggregations were discovered in 1967, they were subjected to intense fishing effort first by Soviet trawlers (Komrakov 1970) and 2 years later by Japanese trawlers (Sasaki 1986). The combined annual catch of armorhead rapidly increased and reached a high of 164,000 metric tons (t) in 1973 (Borets 1975, Takahashi and Sasaki 1977) before plummeting to 875 t in 1978. This decline in catch was evidently due to a decline in armorhead abundance, because the Japanese catch-per-unit-effort (CPUE) showed a corresponding drop from a high of 54.0 t/hr in 1972 to 0.4 t/hr in 1978 (Sasaki 1986).

Although never a participant in this fishery, the United States became involved in 1976 when implementation of the Magnuson Fishery Conservation and Management Act extended its exclusive economic zone (EEZ) to include the Hancock Seamounts, the southernmost of the SE–NHR seamounts supporting the armorhead fishery. Although Soviet trawlers ceased operations on the Hancock seamounts after the jurisdictional change, Japanese trawlers continued to fish but were subject to an annual harvest quota and were required to carry U.S. observers who monitored the catch. Regardless of these management efforts, catch rates continued to decline and the Japanese discontinued fishing on the Hancock Seamounts in 1984. In response to the apparent stressed condition of the armorhead population, the National Marine Fisheries Service (NMFS) in 1985 initiated a stock

Manuscript accepted 5 July 1992.
Fishery Bulletin, U.S. 90:756–769 (1992).

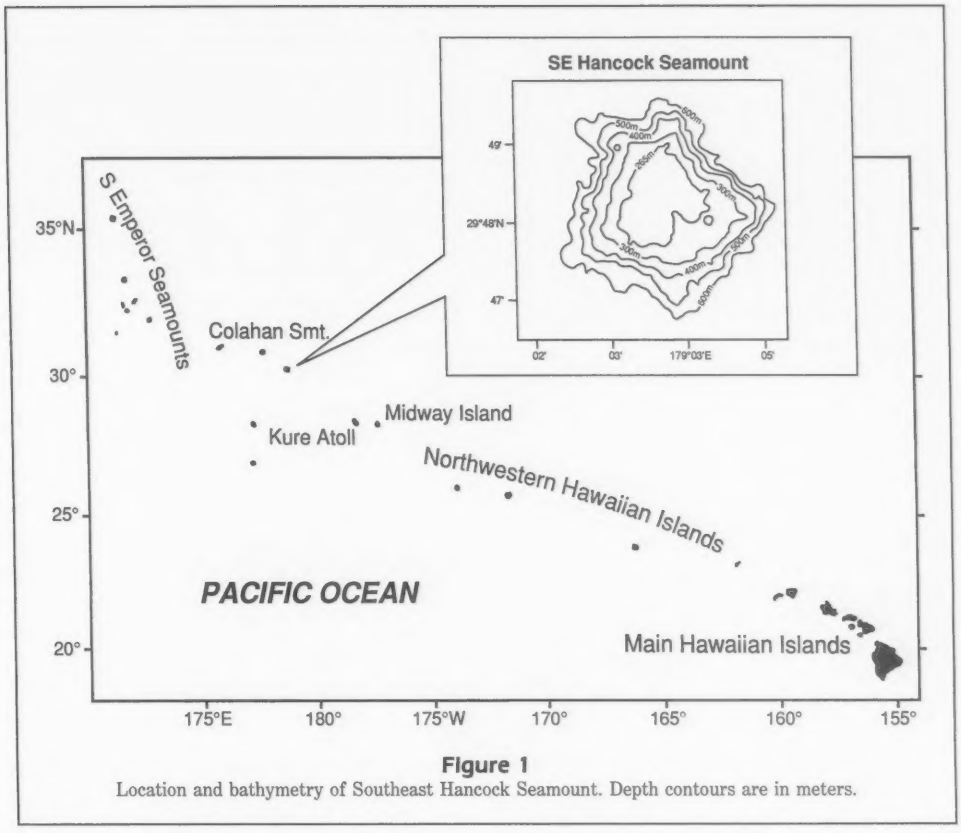


Figure 1
Location and bathymetry of Southeast Hancock Seamount. Depth contours are in meters.

assessment program to monitor armorhead abundance, and in 1986 enacted a 6-yr moratorium prohibiting trawl fishing on the Hancock Seamounts.

The population dynamics of pelagic armorhead have been previously examined (Borets 1975, Wetherall and Yong 1986); however, the results of these studies are questionable because they were based on either Soviet or Japanese catch-and-effort statistics but not both. The present paper attempts to rectify the problem of incomplete data by focusing solely on the stock of armorhead inhabiting the Southeast (SE) Hancock Seamount, where catch-and-effort statistics were supplemented with various biological and vessel performance data after the initiation of the U.S. observer program in 1977 and were completely replaced by research stock-survey data when the commercial fishery ended. With these additional data, it is possible to obtain absolute estimates of armorhead abundance, rather than relative estimates, and to extend the time-series of such estimates beyond the termination of the commercial fishery. In addition to developing a continuous record of armorhead abundance since the initiation of the fishery, this paper also includes estimates of the natural mortality rate and annual recruitment of pelagic juveniles to the seamounts.

Materials and methods

SE Hancock Seamount

The Hancock seamounts consist of two peaks, Northwest (NW) and SE Hancock Seamount, separated by 61 km and situated on the NHR ~293 km northwest of Kure Atoll, the northernmost of the Hawaiian Islands, and ~287 km southeast of Colahan Seamount, the closest seamount supporting an armorhead fishery (Fig. 1). The SE Hancock Seamount is shaped somewhat like a truncated cone with a relatively flat, smooth summit and steep, rugged flanks (Fig. 1). This topography, combined with the tendency of armorhead to nocturnally migrate from the flanks to the summit (Humphreys and Tagami 1986), constrained the commercial trawl fishery to operate primarily on the summit (<300 m) at night (Sasaki 1986).

Types of data and preliminary analysis

Since the types of data available for describing the population dynamics of armorhead have changed with time, it is convenient to separate the entire 1970–90 interval into three periods: (1) 1985–90, when NMFS stock surveys were conducted but no commercial fishing occurred; (2) 1978–84, when regulated Japanese fishing occurred with U.S. observers aboard the vessels; and (3) 1970–77, when unregulated Japanese and Soviet fishing occurred.

Period 1 In the period 1985–90, NMFS conducted 10 armorhead stock-survey cruises to SE Hancock Seamount. Although bottom trawls were occasionally used, the primary sampling gear was a bottom longline. Unlike trawls, longlines could be used on the steep flanks of the seamount and allow sampling of the entire population. Longlines consisted of 30 rigid poles (droppers), each with 5 equally-spaced hooks on short leaders, attached at 18m intervals along a 600m groundline (Shiota 1987). On all cruises, longlines were set perpendicular to the depth contours to maximize the depth range sampled and were fished with the same bait (squid), hook size (no. 20 circle), soak time (1 hr), and fishing period (0800–1830 hr) to maintain constant catchability. Starting in 1986, however, catchability changed slightly when hook timers (small timing devices that are activated when a fish strikes the hook; Somerton et al. 1989) were installed on the leaders. To estimate the effect of timers on armorhead catchability, a comparison experiment was conducted in 1990 in which droppers were alternated with and without timers along the longline. A correction coefficient accounting for the effect of timers on catchability was then estimated as the ratio of the armorhead catches for droppers with timers to those without timers (this ratio was 0.77).

Since preliminary information indicated that armorhead density varied with depth on the seamount, stock surveys were based on a depth-stratified sampling design. Fishing depths were estimated by recording a depth profile of the bottom as the longline was set, then partitioning the measured distance between the terminal anchors into 30 equal intervals (the number of droppers). To help correct for possible differences between fathometer depths and actual fishing depths due to horizontal drift while the longline sank, maximum depth recorders were placed on both anchors and at the midpoint of all longline sets. Recorded maximum depths were used instead of fathometer depths to determine where the anchors and midpoint lay along each depth profile.

When longlines were retrieved, the species identity of each captured fish was recorded along with the number of the hook on which it was caught. All fish from each 5-dropper segment of the longline were then placed together into a basket for later collection of the following biological attributes: sex, fork length (FL, mm), and body depth (BD, mm) which is the shortest distance between the bases of the first anal spine and the dorsal fin. In 1985, body weight (W, g) was also measured on some specimens in addition to body depth. Equations predicting BD from W and FL, and predicting W from BD and FL, were calculated from these data by using multiple regression. These equations are:

Females (n 436)

BD	86.69 − 0.19FL + 0.10W	(R^2 0.91)
W	−936.25 + 9.06BD + 2.49FL	(R^2 0.90)

Males (n 476)

BD	75.55 − 0.18FL + 0.10W	(R^2 0.85)
W	−934.02 + 7.52BD + 2.82FL	(R^2 0.87)

Although the depth distribution of armorhead on the longline could be determined unambiguously with the sampling procedure used, this was not true for the depth distribution of any of the measured or derived biological attributes, because the catch from each 5-dropper segment was aggregated before the attributes were measured. As a means of approximating such depth distributions, the biological attributes of individual fish within each segment group were randomly assigned to the capture depths within the segment.

The relative abundance of armorhead during each stock-assessment cruise was expressed as the mean catch in numbers per hook ($\bar{U}$) estimated as a weighted average over four depth strata (<265, 265–300, 301–400, 401–500m). Algebraically, ($\bar{U}$) is

$$\bar{U} = \frac{\sum_{i=1}^{4} U_i A_i}{\sum_{i=1}^{4} A_i}, \quad (1)$$

where U_i is the catch per hook, and A_i is the bottom area in depth stratum i. Values of U_i were corrected for the influence of hook timers, and values of A_i were estimated as planar areas between the strata depth boundaries measured on a bathymetric map of the SE Hancock Seamount (Fig. 1).

Since armorhead begin to lose weight after arriving at the seamounts, we examined an index of relative fatness (FI), defined as body depth divided by fork length, as an index of post-recruitment age. Frequency distributions of FI were calculated as weighted averages, where the weighting factors were proportional to the estimated abundance of armorhead in each depth stratum. Algebraically, this is expressed as

$$\bar{N}_{\cdot j} = \frac{\sum_{i=1}^{4} N_{ij} A_i U_i}{\sum_{i=1}^{4} A_i U_i}, \quad (2)$$

where N_{ij} is the number of fish in FI category j and depth stratum i.

The frequency distributions of FI usually display two or three distinct modes which are similar in appearance to the modes often present in length-frequency distributions of temperate fishes. Since armorhead recruitment to the seamounts is seasonal (Boehlert and Sasaki 1988), these modes were assumed to represent annual cohorts of fish. To estimate the proportion of the population contributed by each cohort (P_k) and the mean and variance of its FI distribution, the FI distributions were separated into their component distributions by fitting a distribution mixture model using a procedure developed for length-frequency data (Macdonald and Pitcher 1979).

Several of the year-class modes in the FI distributions were so distinct that they could be followed through the time-series in an orderly progression from when they were fat (high FI) to when they were lean (low FI). This feature of the FI distributions was used in two ways. First, the rate at which armorhead decrease in fatness was estimated by following the particularly strong year-class recruiting to the seamount in 1986. Mean FI of this cohort (μ_k) on each cruise was regressed against the time (in months), and the time squared, since the cohort was considered fully recruited to the seamount. Linearity of the relationship was determined by the significance of the coefficient of the squared term.

Second, the instantaneous natural mortality rate (M) of armorhead was estimated by following two cohorts, one composed of armorhead recruiting to the seamount in 1986 and the other composed of all armorhead present on the seamount during the first cruise in 1985. Relative abundance of each cohort at each time (t) was first estimated as the product of the catch-per-hook and the proportion of the population within the appropriate cohort on each cruise; that is, $P_{k,t}\,\bar{U}_t$. Instantaneous natural mortality rate was then estimated by regressing the natural logarithm of relative abundance against the time (in months) since the cohort was considered fully recruited. Analysis of covariance (ANCOVA) was used to test whether the slopes of the regression lines (i.e., the estimated values of M) differed between cohorts. A best estimate of M was computed as the average of the estimates for the two cohorts weighted by the inverses of their variances. Additionally, M was estimated for each sex separately, considering only the 1986 cohort. ANCOVA was again used to test whether the estimated values of M differed between sexes. These and all subsequent applications of ANCOVA herein will first test a model with one slope and two intercepts against a model with two slopes and two intercepts. If such a test is not significant, then a model with one slope and one intercept is tested against a model with one slope and two intercepts.

Period 2 In the period 1978–84, Japanese trawlers conducted 10 fishing trips to SE Hancock Seamount. For all trips, U.S. observers recorded the weight of armorhead caught and the duration of each trawl-haul. In addition, fork length and body weight were recorded for a random sample of armorhead drawn from each haul.

The biomass of armorhead at the start of each fishing trip was estimated by using the Leslie method (Leslie and Davis 1939) in which the change in CPUE over time is related to the cumulative catch removed. Algebraically, this is expressed as

$$U_d = B_0\, q - q\, K_d, \quad (3)$$

where U_d is the daily average catch (in kg) of armorhead per hour of fishing on day d, K_d is the cumulative catch of armorhead up to the beginning of day d, q is the catchability coefficient, and B_0 is the initial biomass. Two parameters (q, B_0) were estimated by regressing U_d on K_d; variance of B_0 was estimated using the equation from Polovina (1986). Mean catchability, $\bar{q}_j$, and its variance were calculated from the per-trip estimates.

Frequency distributions of FI were computed the same as for Period 1, except that body depths were not measured but were estimated from body weights and fork lengths using the regression equation previously described. Since the distributions showed apparent cohort modes similar to those observed during Period 1, the mean and variance of the FI distribution for each cohort and the proportional contribution of the cohort to the population were again estimated with a distribution mixture model. The rate at which FI decreased with time was estimated by regressing the mean FI of the cohort recruiting in 1980 against the time (in months), since the cohort was considered fully recruited.

Period 3 In the period 1970–77, Japanese trawlers fished Hancock Seamounts for at least 1 month in every year; however, data from NW and SE Hancock Seamounts could not be separated. Soviet trawlers also likely fished the Hancock Seamounts over this period, but the available Soviet data (Borets 1975) were aggregated over all seamounts and were not useful for determining the stock dynamics on the Hancock Seamounts.

Relative abundance of armorhead was therefore based solely on Japanese data and was calculated as the reported monthly catch divided by the fishing effort (in hr). Annual mean catch-per-hour ($\bar{U}_t$) and its variance were calculated from the unweighted monthly means. FI could not be calculated during this period due to insufficient data.

Biomass estimation

Armorhead abundance could be estimated in absolute terms as biomass only in Period 2. In the other periods, abundance was estimable in relative terms as CPUE. To allow estimation of biomass from CPUE in Periods 1 and 3 and to allow the merging of all three periods into one continuous time-series, several parameters were required that could be estimated only with data from Period 2. For this reason, we will start by describing the biomass estimation procedures for Period 2.

Period 2 The initial biomass estimates obtained for Period 2 (i.e., Leslie estimates of initial biomass in each year, $B_{0,t}$) may not include the total biomass of armorhead on the SE Hancock Seamount. Instead, the initial estimates may include only the biomass of the fishable stock or that portion of the stock occurring on the summit at night and therefore vulnerable to trawls. The question of whether $B_{0,t}$ includes the total population was addressed by testing the equality of two different estimators of annual recruitment to the seamount. The first (R_1) was calculated as the difference between the estimated biomass in 1 year minus the expected biomass surviving from the previous year. Assuming that the catch was taken in a brief interval at the start of the year, this relationship can be expressed as

$$R_{1,t+1} = B_{0,t+1} - (B_{0,t} - C_t)\, e^{-M}, \quad (4)$$

where $B_{0,t}$ and $B_{0,t+1}$ are the biomass estimates in years t and t+1, C_t is the catch in year t, and e^{-M} is the annual survival rate. The second (R_2), is calculated as the proportion of the biomass composed of recently recruited fish:

$$R_{2,t+1} = B_{0,t+1}\, P_{r,t+1}, \quad (5)$$

where $P_{r,t+1}$ is the proportion of the population composed of the cohort recruiting in year t+1. If $B_{0,t}$ estimates include the total biomass, then they will be appropriately scaled to C_t, and R_1 will equal R_2. But if the $B_{0,t}$ estimates are less than the total biomass, then R_1 will be greater than R_2. Equality was tested using the statistic

$$Z = \frac{R_1 - R_2}{\sqrt{\mathrm{Var}\,(R_1 - R_2)}}, \quad (6)$$

where Z was assumed to be distributed as a normal random variable. Estimates of $\mathrm{Var}(R_1 - R_2)$ were computed as described in the Appendix.

The fishable proportion of the stock (P_f) was estimated in two stages. First, total biomass of the 1980 cohort was estimated for each year in 1980–84, when the 1980 cohort represented more than 90% of the total population, by using an age-structured analysis (Megrey 1989) applied to a single cohort. Starting with a known or assumed value of biomass at the beginning of 1985, this analysis sequentially predicts biomass in each preceding year by accounting for catch and natural mortality. If the catch occurs over a short period at the start of the year, total biomass of this cohort in each year (B^*_t) can be expressed as

$$\begin{aligned} B^*_{t0-1} &= B^*_{t0}\, e^{M} + C_{t0-1} \\ B^*_{t0-2} &= B^*_{t0-1}\, e^{M} + C_{t0-2} \\ &= B^*_{t0}\, e^{M} + C_{t0-1}\, e^{M} + C_{t0-2} \quad (7) \\ &\vdots \\ B^*_{t0-n} &= B^*_{t0}\, e^{nM} + \sum_{i=1}^{n} C_{t0-1}\, e^{(n-i)M}, \end{aligned}$$

where B^*_{t0} is an estimate of total biomass at the start of the last year (t_0) in the time-series (terminal biomass), and C_{t0-i} is the catch in year t_{0-i}. Second, the proportion fished in each year ($P_{f,t}$) was then estimated as $B_{0,t}/B^*_t$, and mean P_f was then estimated as the average of the five annual estimates. This estimate of P_f, however, was not unique because it depended on B^*_{t0}, and B^*_{t0} was chosen arbitrarily because no independent estimate was available. Therefore, the terminal biomass B^*_{85} (the terminal fishing year was defined as 1985 as a later convenience) was estimated along with P_f. Assuming P_f is a constant, the two parameters were estimated by minimizing the weighted sum of squares of the $P_{f,t}$ with weights equal to the inverse of the variance of each $P_{f,t}$.

Once the estimate of mean P_f had been obtained, corrected estimates of the initial biomass in each year (i.e., corrected Leslie estimates) were estimated as

$$B^*_{0,t} = \frac{B_{0,t}}{P_f}, \quad (8)$$

and the mean annual biomasses were then estimated as

$$B^*_t = \frac{U_t}{q_t P_f}, \quad (9)$$

where U_t and q_t are the mean annual CPUE and catchability. Variance of B^*_t was estimated with methods described in the Appendix.

Period 3 Biomass during Period 3 was estimated from the mean catch-per-hour of Japanese trawlers (U_t) as

$$B^*_t = \frac{U_t}{q_j P_f}, \quad (10)$$

where q_j is the mean catchability of Japanese trawlers estimated for Period 2. Variance of B^*_t was estimated with methods described in the Appendix.

Period 1 Biomass during Period 1 was estimated from longline catch-per-hook (U_t) as

$$B^*_t = \frac{U_t W_t}{q_l}, \quad (11)$$

where W_t is the mean individual weight of armorhead caught during sampling Period t, and q_l is the catchability of the longlines. Estimation of q_l required an independent estimate of B^*_t for at least one of the sampling periods, and the estimate chosen was the terminal biomass of the 1980 year-class in 1985. Catchability was thus estimated as

$$q_l = \frac{U_{85} P_{80} W_{85}}{B^*_{80,85}}, \quad (12)$$

where U_{85} is the catch-per-hook, W_{85} is the mean body weight in 1985, $B^*_{80,85}$ is the terminal biomass of the survivors of the 1980 year-class at the start of 1985, and P_{80} is the proportion of the 1985 population composed of the 1980 year-class survivors. Variances of B^*_t and q_l were estimated with the methods described in the Appendix.

Spawning and recruitment biomasses

Spawning and recruitment biomasses were estimated for Periods 1 and 2 in which FI information was available. Spawning biomass in each year (S_t) was estimated as:

$$S_{t+1} = \left(B^*_t - \frac{C_t}{2}\right) e^{-\frac{M}{2}} (1 - P_{r,t}), \quad (13)$$

where $P_{r,t}$ is the proportion of B^*_t comprised of newly-recruited fish, and all other terms are as previously defined. This formulation assumes that B^*_t was always estimated on 1 July, the midpoint of both the fishing season and the stock-assessment cruise. Natural mortality between 1 July and 31 December, the assumed peak of spawning (Bilim et al. 1978), was accounted for by the term $e^{-M/2}$, where M is the annual instantaneous natural mortality rate. $P_{r,t}$ was estimated as the proportion of the population (P_k) within the modal group with the largest mean FI, or as zero if no model group had a mean FI>0.25. $P_{r,t}$ was included in the estimate of spawning biomass because, based on samples collected on the August 1988 stock-assessment cruise (R. Humphreys, NMFS Honolulu Lab., unpubl. data), female armorhead appear to be nonreproductive during the first spawning season after they recruit to the seamounts. Recruitment biomass was estimated as

$$R_t = \left(B^*_t + \frac{C_t}{2}\right) P_{r,t}. \quad (14)$$

This formulation assumes that recruitment occurs from March to May (Boehlert and Sasaki 1988) and is complete by the time B^*_t is estimated. Since young armorhead recruit to the seamounts at approximately 24–30 months of age (Uchiyama and Sampaga 1990), recruitment follows spawning by 3 calendar years. Spawner-recruit relationships were therefore examined using a 3-year lag between spawning and recruitment.

Results and discussion

The armorhead population on SE Hancock Seamount fluctuated tremendously between 1970 and 1990 (Fig. 2) and declined steadily after the population high in 1972, except for small increases occurring in 1980 and 1986. Before the forces producing these changes (i.e., natural mortality, fishing mortality, and recruitment) are examined, the potential biases and the precision of the biomass time-series will be considered.

Biomass estimates

Construction of the time-series of biomass estimates required (1) merging two time-series of CPUE data that were non-overlapping in time and were from distinctly different gear types, and (2) the conversion of a relative measure of abundance (CPUE) into the absolute measure of biomass. Since Japanese trawls and research longlines were never used simultaneously, the time-series could not be merged by simply standardizing the catchability of one gear relative to the other. Fortunately, however, the armorhead popula-

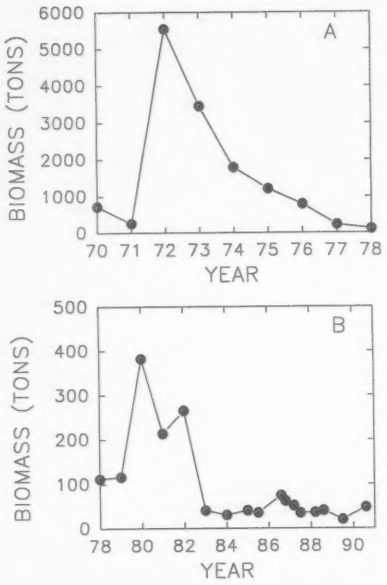


Figure 2

Pelagic armorhead *Pseudopentaceros wheeleri* biomass on Southeast Hancock Seamount during periods of (A) high abundance (1970–78) and (B) low abundance (1979–90). Prior to 1985, when routine stock-assessment surveys were initiated, the biomass estimates are annual means and are shown at the beginning of the year. Starting in 1985, the biomass estimates are for each stock-assessment survey and are shown for the appropriate month.

tion on SE Hancock seamount was sufficiently small and the fishing effort was sufficiently large to allow use of the Leslie method to estimate both the mean catchability of the trawlers (q_j) and the biomass at the initiation of each fishing season ($B_{0,1}$) during the period just prior to replacement of commercial trawling by research longlining. The time-series was merged by using the estimate of q_j and P_f to compute biomass from Japanese trawl CPUE and by using the estimates of $B_{0,t}$ to estimate q_l and thereby compute biomass from longline CPUE. Thus, the Leslie method provided the means to merge the two time-series and to express the resulting time-series in terms of biomass.

Because success of this procedure rests on the successful application of the Leslie method, any biases in the biomass estimates are likely the result of violations of the underlying assumptions. One of the most important assumptions of the Leslie method is that the change in size of the population is solely due to removals by the fishery. In practice, this requires that the population is closed to immigration and the fishery is sufficiently short and intense so that the effect of natural mortality is negligible. In nearly all cases examined, these requirements were met; that is, fishing usually occurred well after the spring peak in recruitment of pelagic juveniles (Table 1; Boehlert and Sasaki 1988) and the catch was usually obtained in 1 or 2 months and represented a large fraction of the estimated biomass (Table 1). One further indicator of the successful application of the Leslie method is the significance of the slope of the regression, or q. Although the estimates of q obtained using the Leslie method were not always significantly greater than zero, they were remarkably similar among years for each vessel that had fished repeatedly (Table 1). Such similarity was used as justification for using the non-significant estimates in later calculations.

Table 1

Leslie estimates of initial biomass (B_0) and catchability (q) of pelagic armorhead *Pseudopentaceros wheeleri* for each of the Japanese fishing trips during Period 2 (1978–84) on SE Hancock Seamount.

Year	Month	Vessel ID no.	Days fished	Catch (t)	B_0 (t)	q	$P(q=0)$
1978	May	1	11	204	198	0.00197	<0.001
1979	Jun	2	18	68	80	0.00059	<0.005
1980	Aug	3	29	453	551	0.00047	<0.001
1981	Jun	2	5	161	297	0.00101	>0.10
	Aug	3	20	44	55	0.00067	>0.10
1982	May	4	10	180	269	0.00064	0.10
	Jul	2	12	8	17	0.00071	>0.10
1983	Jul	3	19	39	38	0.00066	<0.001

Bias could also result from violation of another assumption of the Leslie method, that the entire population is equally vulnerable to the sampling gear. Such bias was considered likely when initial biomass estimates from Period 2 seemed too small to be consistent with the observed catches. This apparent inconsistency was examined statistically by testing the equality of two estimators of recruitment, one that included catch (R_1; Eq. 4), and one that did not (R_2; Eq. 5). The bias was confirmed since in 4 of the 5 years examined, R_1 was significantly ($P<0.05$) greater than R_2, a condition that could occur only if the biomass estimates were too small.

The most likely explanation for the underestimation of armorhead biomass is that the $B_{0,t}$ estimates do not include the entire population and instead include only the fishable population or the part actually exposed to trawls. This result was surprising because we believed that the population would be sufficiently mixed by the nocturnal vertical migration so that all armorhead would be equally vulnerable even though the trawls were topographically restricted to only a part of the armorhead depth range. Our

finding, however, indicates either that mixing is minimal or that the rate of mixing is relatively low compared with the 2- to 4-week duration of a typical Japanese fishing trip.

Although the bias in $B_{0,t}$ was corrected by estimating the proportion of the stock vulnerable to trawling (P_f= 0.27), adequacy of this correction rests on the assumption that P_f does not vary with time. However, P_f may vary with time because the depth distribution of armorhead may vary. For example, the proportion of the population occurring in the shallowest depth stratum (<250 m) averaged 15% over the 10 research cruises, but ranged from 0 to 40%. It is unclear if such variation in the daytime distribution is reflected in the nighttime distribution, because armorhead do not feed at night and therefore cannot be sampled effectively with longlines (M.P. Seki and D.A. Somerton, NMFS Honolulu Lab., unpubl. data). Bias in the biomass estimates could additionally occur if P_f depends on the degree of mixing of deep and shallow fish, because P_f would likely be larger when fishing periods were longer and less intense. Since fishing periods tended to be longer during Period 3 than in Period 2, this would lead to an overestimate of biomass during Period 3.

Precision in the estimates of biomass, which is expressed as the coefficient of variation (CV) to compensate for the large range in biomass, was smallest in Period 1 (Fig. 3), because longline CPUE estimates were more precise than trawl CPUE estimates. Expressed differently, based on the mean CV over the period 1970–84 (excluding 1971 when data were not sufficient to estimate the variance of U_t), the 95% confidence intervals for B^*_T was $\pm 1.70\ B^*_T$, which in all years includes zero. Over the period 1985–90, however, the 95% confidence interval was $\pm 0.29\ B^*_T$, and never included zero.

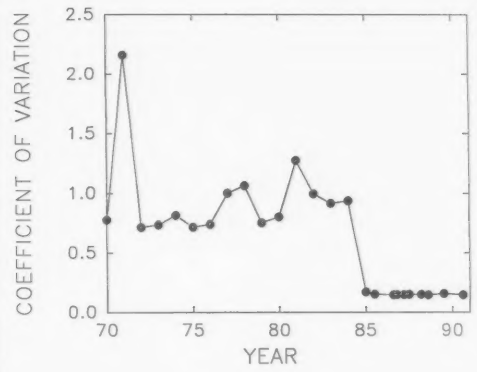


Figure 3
Coefficient of variation of the biomass estimates of pelagic armorhead *Pseudopentaceros wheeleri* as a function of time.

Post-recruitment ageing

The estimates of natural mortality rate and annual recruitment required estimates of the age distribution. Although the ages of armorhead can be determined using either daily or annual growth increments on their otoliths (Uchiyama and Sampaga 1990), they are easily obtainable only for individuals in the pelagic phase of their life history, because somatic growth ceases once armorhead recruit to the seamount (Humphreys et al. 1989) and growth increments become so closely spaced that they are exceedingly difficult to count (R. Humphreys, NMFS Honolulu Lab., pers. commun.). Thus, we expressed age on a scale relative to the presumed time of recruitment. Such post-recruitment ages were based on the decrease in FI over time.

Frequency histograms of FI display modes which can be tracked sequentially from one histogram to the next over time as they move from the right (high FI or fat) to the left (low FI or lean). Two examples of this are the large mode that appeared in 1980 and could be followed until 1984 (Fig. 4A) and the large mode that appeared in 1986 and could be followed until 1990 (Fig. 4B). Since the first appearance of these modes was always associated with an increase in CPUE (Fig. 2B), they were interpreted to represent cohorts of fish that had recruited to the seamount.

To further substantiate our interpretation of the modes, the rate of decrease in FI was examined for consistency both over time and between the two presumed year-classes. Plots of FI versus time appeared to have slight curvature (Fig. 5), but for both the 1980 and 1986 year-classes the curvature was not significant ($P>0.05$). Changes in FI, therefore, are proportional to changes in post-recruitment age. The rates of decrease in FI of the 1986 (0.00169/mo) and the 1980 (0.00157/mo) year-classes did not differ significantly (ANCOVA, $P>0.05$). In addition, sexual equality in the rate of decrease in FI was tested for the 1986 year-class alone, and the male rate was not significantly different (ANCOVA, $P>0.05$) from the female rate. Taken together, these findings indicate that all armorhead decrease in FI at approximately the same rate and that once established by the recruitment of a strong year-class, the coherency of an FI mode should be preserved over time.

Natural mortality

Natural mortality was estimated from the change in the relative abundance of two cohorts over time during a period when no commercial fishing occurred. The first of these cohorts, which consisted

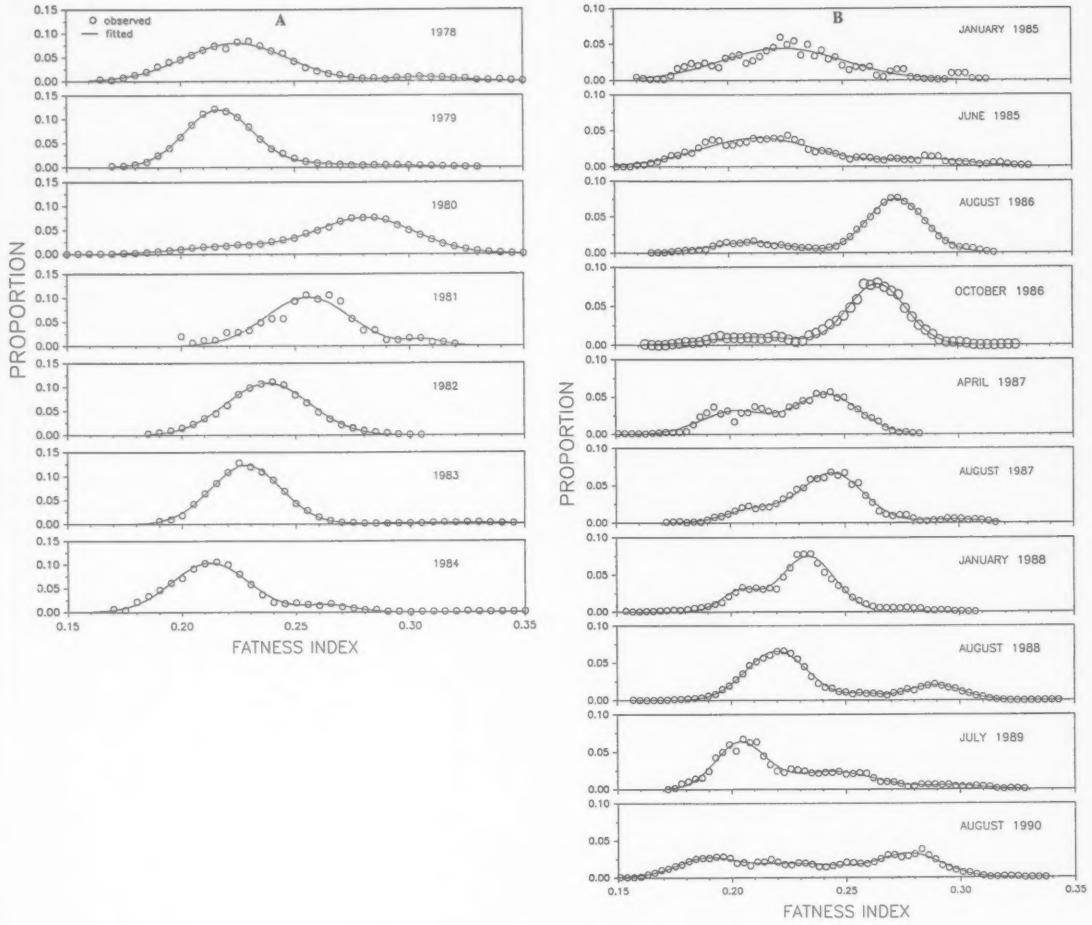
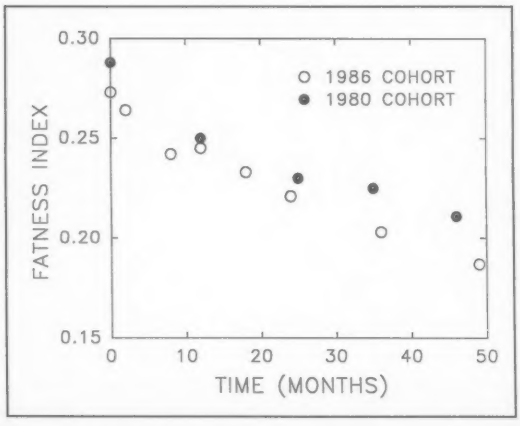


Figure 4

Frequency histograms of fatness index are shown for Japanese commercial catch of pelagic armorhead *Pseudopentaceros wheeleri* in (A) each year during 1978–84 and (B) for each of the research cruises during 1985–90.



of the extant armorhead population in January 1985, was identifiable for seven consecutive samplings and had an instantaneous natural mortality (M) of 0.054/mo. The second, which consisted of the year-class recruiting in 1986, was identifiable for eight consecutive samplings and had an M of 0.044/mo (Fig. 6). Although the two estimates were significantly different (ANCOVA, $P<0.05$), the weighted average (0.045/mo or 0.54/yr) was chosen as

Figure 5

Decrease in fatness index of pelagic armorhead *Pseudopentaceros wheeleri* with time for the 1980 and 1986 year-classes on Southeast Hancock Seamount.

the most representative value. For both cohorts, log-relative abundance was clearly a linear function of time, and M is therefore invariant with age (Fig. 6A).

When M was estimated separately for each sex, considering the 1986 cohort alone, the value for males (0.037/mo) was significantly different (ANCOVA, $P<0.001$) from the value for females (0.045/mo). Furthermore, the intercept of the regression, i.e., the log-relative abundance at the time of recruitment) appeared to be smaller for males (4.27) than for females (4.94), but the difference could not be tested because of the strong difference in slopes (Fig. 6B). Taken together, these results indicate that, at least for the 1986 cohort, females recruited to the seamounts in greater abundance than males but subsequently died at a greater rate. It is also possible that the higher mortality rate of females was primarily restricted to the first year of residence on the seamount (Fig. 6B).

Since a sexual difference in mortality seemed inexplicable to us, we examined the possibility that longlines preferentially selected fat females. This was done by examining whether the ratio of females to males, expressed as proportion female, changed with FI similarly for trawls as for longlines. Since the FI values of females and males decrease identically with time, any change in female proportion with FI would indicate either selective sampling or differential mortality, depending on whether one or both gear types showed the change. To test for such changes, female proportion was regressed on FI for various samples. When these regressions were performed on the longline samples, all 10 had a significant ($P<0.05$) positive slope. When the regressions were performed on the research trawl samples, four of five had a significant positive slope. Thus a sampling bias is unlikely, unless both gears produced a similar bias.

The estimate of natural mortality rate (0.54/yr) is more than twice that reported in Borets (0.25/yr; 1975). His estimate, however, was based on age data that were likely biased for two reasons. First, the age range [i.e., 7 yr, ages 5–12], reported in Borets (1975) appears to be excessive when compared with the range estimated from modal progression through the research FI histograms (4–5 yr). Second, the mean age of the catch between 1968 and 1974 reported in Borets (1975) did not decrease as would be expected in a developing fishery. On the other hand, our estimate of natural mortality rate was less than the rate implied in the studies of Uchida and Tagami (1984), Humphreys et. al. (1989), and Uchiyama and Sampaga (1990), which all suggested that armorhead were semelparous and, like Pacific salmon *Oncorhynchus* spp., died soon after spawning.

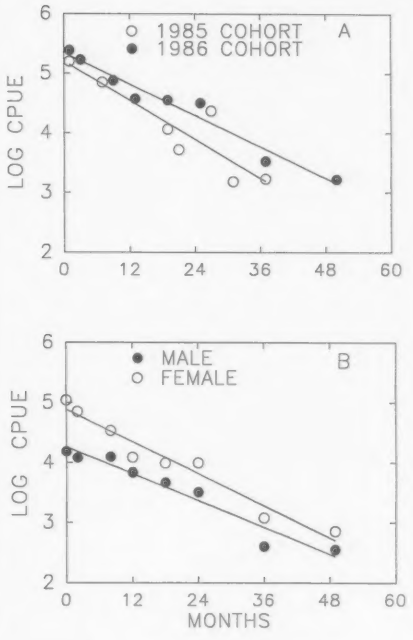


Figure 6

Change in log CPUE of pelagic armorhead *Pseudopentaceros wheeleri* versus time for the (A) cohort composed of the extant population in 1985 and the cohort recruiting in 1986, and (B) for males and females of the 1986 recruiting cohort.

Fishing mortality

Fishing mortality rate (F) can be estimated only between 1978 and 1983 when the total catch and effort on SE Hancock Seamount are known with reasonable certainty, based on the U.S. observer program. Over this period, F, which was calculated as the estimated value of $q_j \times$ total annual effort, averaged 1.03/yr or roughly twice the natural mortality rate. The mean exploitation rate (which was approximated as $(F/Z)(1-e^{-Z})$ where $Z=F+M$), was ~0.50. Therefore, provided that no recruitment occurred and that fishing effort was continuous throughout the year, then an average of roughly 50% of the population at SE Hancock Seamount was removed annually by the fishery over this period.

Recruitment

Annual recruitment to SE Hancock Seamount was extremely intermittent between 1978 and 1990. When expressed in metric tons, the 1980 recruitment clearly dominated the entire record (Fig. 7A). However, the total biomass changed considerably over this period, and, when expressed as a percentage of the total biomass, the 1986 recruitment and—to a lesser extent—the 1988 and 1990 recruitments were also relatively important (Fig. 7B). For some

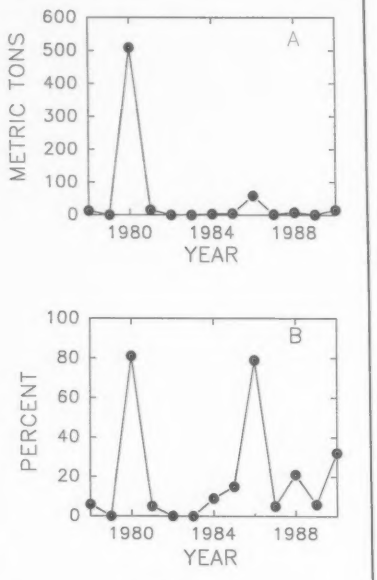


Figure 7
Annual recruitment to Southeast Hancock Seamount expressed in (A) metric tons and (B) percent of the population biomass of pelagic armorhead *Pseudopentaceros wheeleri*.

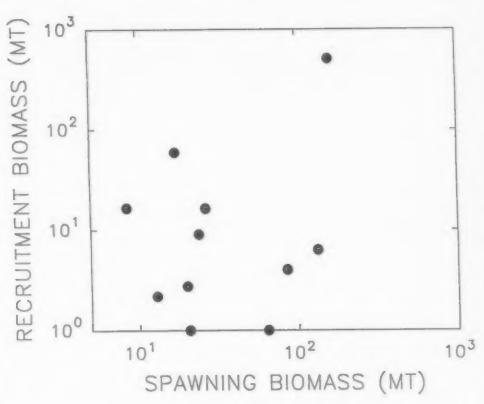


Figure 8
Annual recruitment versus spawning biomass of pelagic armorhead *Pseudopentaceros wheeleri* 2 years earlier.

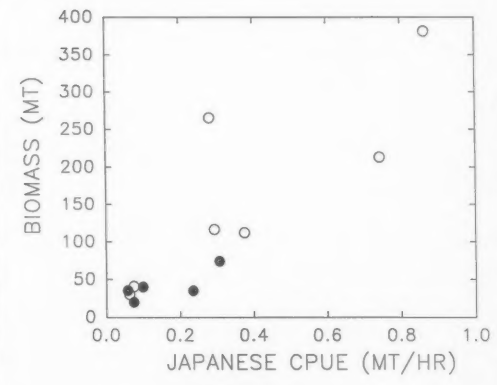


Figure 9
Biomass of pelagic armorhead *Pseudopentaceros wheeleri* on Southeast Hancock Seamount and Japanese trawl catch/hr on all other southern Emperor–northern Hawaiian Ridge seamounts during (●) Period 1 (1985–90) and (○) Period 2 (1978–84) when the Southeast Hancock Seamount population experienced fishing.

unknown reason, recruitment in the even years tended to be larger than it was in the odd years (Mann-Whitney test, $P = 0.06$).

Prior to 1978, it is difficult to estimate annual recruitment because the data required to calculate FI were not routinely collected. However, an examination of the large increase in abundance in 1972 (Fig. 2A) cannot be avoided. Interpretation of the 1972 increase is troublesome because the evidence for an unusually large recruitment is equivocal. A large recruitment, for example, should have resulted in a large increase in the proportion of the population comprised of fat armorhead as it did in 1980 and 1986 (Fig. 4A, B), yet the proportion of the population categorized as fat during the period of maximum recruitment was smaller in 1972 than it was in 1973 when recruitment did not appear to be exceptionally large (Boehlert and Sasaki 1988). Armorhead measured in 1972, however, were markedly smaller than in any other year (Takahashi and Sasaki 1977, Borets 1975). One proposed explanation for the small size is that the tremendous abundance of armorhead in 1972 resulted in a density-dependent suppression of growth in the pelagic phase (Borets 1977). This might also have reduced the FI of recruits and thereby masked the FI signature of a large recruitment.

An alternate explanation for the 1972 increase in abundance is that it is an illusion due to a rapid increase in trawl catchability as the newly-developed fishery progressed from an exploratory phase to a production phase (Takahashi and Sasaki 1977, Uchida and Tagami 1984). If, however, the 1972 increase was due simply

to changing catchability, then such an increase should not be evident in the Soviet catch-and-effort data, because the Soviet fishery had developed earlier and was likely beyond its "fishing-up" phase. Soviet data do display an increase from 1971 to 1972 (73–104 million fish/vessel day; Borets 1975), but this is considerably less than that experienced by the Japanese fishery. Thus, it is not entirely clear whether the apparent increase in 1972 was real and due to recruitment or an artifact due to changing catchability.

The dependance of recruitment on spawning biomass was examined by Wetherall and Yong (1986) and found to be essentially nonexistent, at least at the high levels of spawning biomass extant during 1969–77. Recruitment, however, must ultimately be limited by spawning biomass at low population levels; therefore, we reexamined the relationship over the period 1980–90, when the spawning biomass was considerably lower. This was done by plotting, on a log-log scale, the estimated spawning biomass on SE Hancock Seamount against the estimated recruitment 2 years later (Fig. 8). Since a clear relationship is not evident, it is possible that recruitment and spawning biomass are only weakly related even at the low population levels examined. There are, however, at least two other possible reasons why no relationship was found. First, since no apparent genetic difference exists among the armorhead collected at the various seamounts (Borets 1979), recruits to SE Hancock Seamount are likely the progeny of the entire North Pacific population. If the SE Hancock Seamount population does not vary concordantly with the entire North Pacific population, any relationship between recruitment and spawning biomass would be obscured. However, plots of the estimated biomass on SE Hancock Seamount against Japanese CPUE on all SE–NHR seamounts show a strong concordance (Fig. 9). Second, if spawning biomass does exert an influence on recruitment, it may do so only by limiting the maximum level attained. Thus, at higher levels of spawning biomass, higher levels of recruitment are possible—but not assured—because of environmental variability. One interpretation of Figure 8 could therefore be that recruitment did increase with spawning biomass, but at the higher levels of biomass there were several environmentally-poor recruitment years.

Management implications

Since armorhead do not grow after they recruit to the fishery and therefore cannot be growth-overfished, management strategies could be designed solely to achieve some optimum level of spawning stock biomass (SSB). One approach is to define this optimum SSB by using a spawner-recruit relationship as is done for some species of Pacific salmon (Ricker 1975). Another approach is to define it in terms of a fixed percentage of the equilibrium biomass in the absence of a fishery (Beddington and Cooke 1983). But in either case, the spawning population must include the entire SE–NHR population rather than the small component examined here. In addition, some form of international agreement controlling the armorhead catch will be required before any management measures are effective.

Acknowledgments

We thank George Boehlert, Bob Humphreys, Bill Lenarz, and Jeff Polovina for reviewing the manuscript and offering helpful suggestions.

Citations

Beddington, J.R., and J.G. Cooke
1983 The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 p.

Bilim, L.A., L.A. Borets, and M.K. Platoshina
1978 Characteristics of ovogenesis and spawning of the boarfish on the region of the Hawaiian Islands. *In* Fisheries oceanography, hydrobiology, biology of fishes and other denizens of the Pacific Ocean. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (TINRO) 102:51–57 [in Russ.]. (Engl. transl. 106 by W.G. Van Campen, 1986, 9 p.; avail. NMFS Honolulu Lab.)

Boehlert, G.W., and T. Sasaki
1988 Pelagic biogeography of the armorhead, *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the north Pacific Ocean. Fish. Bull., U.S. 86:453–466.

Borets, L.A.
1975 Some results of studies on the biology of the boarfish (*Pentaceros richardsoni*). Invest. of the biology of fishes and fishery oceanography. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (TINRO, Vladivostok) 6:82–90. (Engl. transl. 97 by W.G. Van Campen, 1984, 9 p.; avail. NMFS Honolulu Lab.)
1977 Dynamics of size-age composition of the boerfish (*Pentaceros richardsoni*). Invest. of the biology of fishes and fishery oceanography. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (TINRO, Vladivostok) 8:65–69 [in Russ.] (Engl. transl. 115 by W.B. Van Campen, 1987, 6 p; avail. NMFS Honolulu Lab.)
1979 The population structure of the boarfish, *Pentaceros richardsoni*, from the Emperor Seamounts and the Hawaiian Ridge. J. Ichthyol. 19:15–20.

Efron, B., and G. Gong
1983 A leisurely look at the bootstrap, the jackknife and cross-validation. Am. Stat. 37:36–48.

Humphreys, R.L. Jr., and D.T. Tagami
1986 Review and current status of research on the biology and ecology of the genus *Pseudopentaceros*. *In* Uchida, R.N., et al. (eds.), Environment and resources of seamounts in the North Pacific, p. 55–62. NOAA Tech. Rep. NMFS 43.

Humphreys, R.L. Jr., G.A. Winans, and D.T. Tagami
1989 Synonymy and life history of the North Pacific pelagic armorhead, *Pseudopentaceros wheeleri* Hardy. Copeia 1989: 142–153.

Komrakov, O.E.
1970 Distribution and fishery of the boarfish (*Pentaceros richardsoni*) in the Hawaiian region. Avail. as Transl. 117 from NMFS Honolulu Lab.

Leslie, P.H., and D.H.S. Davis
1939 An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 8:94–113.

Macdonald, P.D.M., and T.J. Pitcher
1979 Age groups from size-frequency data: A versatile and efficient method of analyzing distributions mixtures. J. Fish. Res. Board Can. 36:987–1001.

Megrey, B.A.
1989 Review and comparison of age-structured stock assessment models from theoretical and applied points of view. *In* Edwards, E.F., and B.A. Megrey (eds.), Mathematical analysis of fish stock dynamics, p. 8–48. Am. Fish. Soc. Symp. 6., Bethesda.

Polovina, J.J.
1986 A variable catchability version of the Leslie model with application to an intensive fishery experiment on a multispecies stock. Fish. Bull., U.S. 84:423–428.

Ricker, W.E.
1975 Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Sasaki, T.
1986 Development and present status of Japanese trawl fisheries in the vicinity of seamounts. *In* Uchida, R.N., et al. (eds.), Environment and resources of seamounts in the North Pacific, p. 21–30. NOAA Tech. Rep. NMFS 43.

Seber, G.A.F.
1973 The estimation of animal abundance. Hafner Press, NY, 506 p.

Seki, M.P., and D.A. Somerton
In prep. Feeding ecology and daily ration of the pelagic armorhead, *Pseudopentaceros wheeleri*, at Southeast Hancock Seamount. NMFS Honolulu Lab., 30 p.

Shiota, P.M.
1987 A comparison of bottom longline and deep-sea handline for sampling bottom fishes in the Hawaiian Archipelago. Admin. Rep. H-87-5, NMFS Honolulu Lab., 18 p.

Somerton, D.A., B.S. Kikkawa, and C.D. Wilson
1989 Hook timers to measure the capture time of individual fish. Mar. Fish. Rev. 50(2):1–5.

Takahashi, Y., and T. Sasaki
1977 Trawl fishery in the central North Pacific seamounts [Kita Taiheiyo chubu kaizan ni okeru tororu gyogryo. Hokuyo sokouo gyogyo—Shiryo (3)] Northern waters groundfish fishery—Data (3). Div. North. Waters Groundfish Resour., Far Seas Fish. Res. Lab., 45 p. [In Jpn.; Engl. transl. 22 by T. Otsu, 1977, 49 p.; avail.NMFS Honolulu Lab.]

Uchida, R.N., and D. Tagami
1984 Groundfish fisheries and research in the vicinity of seamounts in the North Pacific Ocean. Mar. Fish. Rev. 46(2):1–17.

Uchiyama, J., and J. Sampaga
1990 Age and growth of the pelagic armorhead *Pseudopentaceros wheeleri* from the Hancock Seamounts. Fish. Bull., U.S. 88:217–222.

Wetherall, J.A., and M.Y. Yong
1986 Problems in assessing the pelagic armorhead stock on the central North Pacific seamounts. *In* Uchida, R.N. et al. (eds.), Environment and resources of the seamounts in the North Pacific, p. 73–86. NOAA Tech. Rep. NMFS 43.

Appendix

Variances of several of the estimators described in Materials and Methods were approximated by using the Delta method (Seber 1973) and assuming all covariance terms were negligible. Variance of $(R_1 - R_2)$ was estimated as

$$\mathrm{Var}(R_1-R_2) = (P_{r,t+1}-1)^2\,\mathrm{Var}(B_{0,t+1})+(B_{0,t+1})^2\,\mathrm{Var}(P_{r,t+1})+e^{-2M}\,[\mathrm{Var}(B_0,t)+\mathrm{Var}(C_t)+(B_{0,t}-C_t)^2\,\mathrm{Var}(M)], \tag{15}$$

where all variables are defined in text Equations 5 and 6. Variances of $B_{0,t}$ and $B_{0,t+1}$ were computed by using the method in Polovina (1986). Variance of C_t was assumed to be negligible because catch was measured by U.S. observers. Variance of M was estimated as the variance of the slope of the regression of log-relative abundance on postrecruitment age (in years). Variance of $P_{r,t+1}$ was estimated with a bootstrap method (Efron and Gong 1983). Bootstrap estimates were obtained from trawl samples of armorhead biological data by iteratively repeating the following steps: (1) A subsample of n fish from each sample was randomly chosen with replacement, where n is equal to the size of the original sample; (2) an FI frequency distribution was constructed from the subsample; (3) $P_{r,t+1}$ was estimated by fitting the distribution mixture model to the FI frequency distributions. In all cases, variance of $P_{r,t+1}$ was calculated as the variance among 100 bootstrap estimates.

Variance of B^*_t during Period 2 was as

$$\mathrm{Var}(B^*_t) = \left[\frac{1}{q_t P_f}\right]^2 \mathrm{Var}(U_t) + \left[\frac{U_t P_f}{(q_t P_f)^2}\right]^2 \mathrm{Var}(q_t) + \left[\frac{U_t q_t}{(q_t P_f)^2}\right]^2 \mathrm{Var}(P_f) \tag{16}$$

where all variables are defined in Equation (9). Variance of U_t was estimated as the variance among the daily U within each year. Variance of q_t was estimated as the variance of the slope of the Leslie model. When more than one vessel fished in each year, however, variance of q_t was the average of the individual variance estimates weighted by catch.

Variance of P_f was estimated by using a Monte Carlo model. Each iteration of the model consisted of generating a random value of $B_{0,t}$ for each year and a value of M, assuming all were normally distributed with means and variances equal to the original estimated values. With these generated values, B^*_t was estimated for each year with Equation (9) and $P_{f,t}$ was estimated as $B_{0,t}/B^*_t$. Mean estimates of P_f and $B^*_{80,85}$ (B^*_{t0} in Eq. 7), were obtained by using the iterative procedure to minimize the weighted sum of squares of the $P_{f,t}$ estimates. In all cases variances of P_f and $B^*_{80,85}$ were estimated from 100 iterations of the Monte Carlo model.

Variance of B^*_t during Period 3 was estimated using Equation (16) but with q_t replaced by q_j. Variance of U_t was estimated as the variance among the monthly means. Variance of q_j was estimated as the variance among the q estimates in Table 1. Variance of P_f is the same as for Period 2.

Variance of B^*_t during Period 1 was estimated as

$$\mathrm{Var}(B^*_t) = \left[\frac{W_t}{q_1}\right]^2 \mathrm{Var}(U_t) + \left[\frac{U_t}{q_1}\right]^2 \mathrm{Var}(W_t) + \left[\frac{U_t W_t}{q_1^2}\right]^2 \mathrm{Var}(q_1), \tag{17}$$

where all variables are defined in Equation (11). Variance of W_t was estimated from the biological samples from each research cruise. Variance of U_t was estimated as the variance of U among the four depth strata.

Variance of q_1 was estimated as

$$\mathrm{Var}(q_1) = \left[\frac{U_{85} W_{85}}{B^*_{80,85}}\right]^2 \mathrm{Var}(P_{80}) + \left[\frac{U_{85} P_{80}}{B^*_{80,85}}\right]^2 \mathrm{Var}(W_{85}) + \left[\frac{P_{80} W_{85}}{B^*_{80,85}}\right]^2 \mathrm{Var}(U_{85}) + \left[\frac{U_{85} P_{80} W_{85}}{B^*_{80,85}}\right]^2 \mathrm{Var}(B^*_{80,85}), \tag{18}$$

where all variables are defined in Equation (12). Variances of W_{85} and U_{85} were estimated as described above for W_t and U_t. Variance of P_{80} was estimated as described for $P_{r,t+1}$. Variance of $B^*_{80,85}$ was estimated with the previously described Monte Carlo model.

Genetic isolation of previously indistinguishable chinook salmon populations of the Snake and Klamath Rivers: Limitations of negative data

Fred M. Utter
Robin S. Waples
David J. Teel

Coastal Zone and Estuarine Studies Division
Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East, Seattle, Washington 98112

Abstract.–An anomalous inability to distinguish certain geographically-separated chinook salmon *Oncorhynchus tshawytscha* populations of the Snake River and the Klamath River from a survey of 18 polymorphic loci led to a prediction that distinction would ultimately be found through sampling of additional polymorphic loci. Recently published studies involving pertinent groups within each of these rivers included data from an additional 15 polymorphic loci, and therefore allow a reexamination of the relationships between these groups. Comparison of results for the new studies shows the formerly indistinguishable groups from two areas to be as distinct from one another as from other major groupings of the species with a mean genetic distance between populations of each river (0.014) that is double that of the maximum within-group genetic distance. Two newly-resolved gene loci (*mMDH-2** and *sMEP-1**) are particularly good at distinguishing populations from the two rivers. In addition to resolving the anomalous similarity between populations inhabiting geographically separated areas, the new results illustrate the care that must be used in drawing inferences from negative data.

Manuscript accepted 5 July 1992.
Fishery Bulletin, U.S. 90:770–777 (1992).

A variety of characteristics can be useful in distinguishing particular groups of organisms from other related groups. In humans, for instance, major ancestral groups can be identified by heritable morphological traits, as well as by characteristic frequencies of alleles detected by molecular or immunological procedures. Conversely, although two groups lacking any distinguishing characteristics may, in fact, be closely related, the possibility of undetected differences often prevents a conclusive determination of the degree of relatedness. For example, two cryptic species of bonefishes in Hawaii were considered members of a common gene pool until biochemical genetic analysis revealed that the two forms diverged perhaps 20 million years ago (Shaklee and Tamaru 1981). Other examples of genetic distinctions between and within species of fishes previously considered to be homogeneous are listed in Allendorf et al. (1987).

The motivation behind our present study was a puzzling instance of apparent genetic similarity between two geographically separated groups of chinook salmon *Oncorhynchus tshawytscha*. Indigenous chinook salmon from the Klamath River and spring- and summer-run chinook salmon from the Snake River are well differentiated from nearby populations at several protein-coding gene loci (Utter et al. 1989, Bartley and Gall 1990, Waples et al. 1991, Bartley et al. 1992). However, a comparison of the two river groups by Utter et al. (1989) failed to distinguish them despite their substantial geographic separation. The mouths of the Snake and Klamath Rivers are separated by a distance of almost 600 river-ocean miles, and a number of ancestrally distinct groups of populations (Utter et al. 1989) are found in intervening areas.

This apparent genetic similarity was even more puzzling because of substantial life-history differences between chinook salmon from the two rivers. The populations that were not well differentiated in the Utter et al. (1989) study included four spring-run and two summer-run populations from the Snake River and two fall- and one spring-run population from the Klamath River. Utter et al. (1989) also sampled fall-run fish from the Snake River, but this population is genetically quite different both from Snake River spring- and summer-run fish and chinook salmon from the Klamath River. Whereas the fall-run fish migrate to sea as subyearlings, the other populations produce juveniles that spend an additional winter in freshwater and outmigrate as yearlings.

Utter et al. (1989) speculated that the anomalously high degree of genetic similarity between Klamath and Snake River populations was due to coincidentally high frequencies of the same common alleles (possibly a reflection of restricted gene flow among populations and reduced population sizes over an extended time interval) rather than to a recent common ancestral origin. Of the 25 polymorphic loci examined, only 18 were variable in either the Snake or Klamath River groups, and populations from these two areas had the lowest average heterozygosities (0.027–0.045; Utter et al. 1989, App. A) of any populations included in the study. Utter et al. (1989) predicted that additional genetic surveys would ultimately reveal divergent frequencies of alleles in the two areas. If such differences were not found in more extensive studies, alternate explanations for this apparent similarity would be required.

This paper retests and rejects the null hypothesis of no genetic difference between these two groups based on two recently published studies, which sample several new populations and an additional 15 polymorphic loci. Comparison of results for the new studies shows the formerly-indistinguishable chinook salmon populations of the Klamath and Snake River to be quite distinct, with a mean genetic distance between populations of each river (0.014) that is double that of the maximum within-group genetic distance. In addition to resolving the anomalous apparent similarity between these chinook salmon populations of these geographically separated areas, the new results illustrate the care that must be used in drawing inferences from negative data.

Table 1

Collection data for samples of chinook salmon *Oncorhynchus tshawytscha* from the Klamath (K1–K10; Bartley et al. 1992) and Snake (S1–S11; Waples et al. 1991) Rivers. Samples from hatchery stocks are marked by a dagger (†); other samples were from naturally spawning populations. Locations included in the study of Utter et al. (1989) are indicated by an asterisk (*). Run timing indicates the season of entry of adults into freshwater.

Map code	Location	Run timing	Sample size
Klamath River			
K1	Omagar Creek	Fall	100
K2	Blue Creek	Fall	100
K3	Camp Creek	Fall	106
K4	Horse Linto Creek	Fall	100
K5	S. Fork Trinity River	Fall	100
*K6	Trinity River†	Fall	120
K7	Upper Salmon River	Fall	98
K8	Shasta River	Fall	100
K9	Bogus Creek	Fall	128
K10	Iron Gate Hatchery†	Fall	99
Snake River			
*S1	Valley Creek	Spring	99
*S2	Sawtooth Hatchery†	Spring	100
S3	Salmon River	Spring	99
S4	Marsh Creek	Spring	100
*S5	Johnson Creek	Summer	97
*S6	McCall Hatchery†	Summer	100
S7	Secesh River	Summer	92
*S8	Rapid River Hatchery†	Spring	100
S9	Imnaha River	Summer	100
S10	Imnaha Hatchery†	Summer	100
S11	Lostine River	Spring	100

Materials and methods

Our analyses used the data from Bartley et al. (1992) for Klamath River populations and Waples et al. (1991) for Snake River populations; comparisons also were made with earlier data from Utter et al. (1989). Sampling locations included 10 areas from the Klamath River and 11 from the Snake River drainages (Table 1, Fig. 1). Samples of juvenile fish from hatcheries and naturally-spawning populations were collected between 1986 and 1989 for the Klamath River, and 1989 and 1990 for the Snake River. Starch gel electrophoresis for all three studies followed procedures described by Aebersold et al. (1987). The data used in these analyses were part of a larger baseline dataset used by management agencies to help determine natal origins of chinook salmon harvested in mixed-stock fisheries (Shaklee and Phelps 1990).

Genetic nomenclature and abbreviations followed a system suggested by Shaklee et al. (1989). Data were collected from 21 enzyme systems and 30 presumptive gene loci that were polymorphic in at least one of the populations (Tables 2, 3). The observed polymorphisms were attributed to 26 disomic loci and 2 isolocus pairs (*sAAT-1,2** and *sMDH-B1,2**; see Allendorf and Thorgaard 1984). A single, average allele frequency was computed for each isolocus pair for purposes of comparing populations.

Genetic data were analyzed using the BIOSYS program of Swofford and Selander (1981). Analyses included calculation of unbiased pairwise genetic distances between populations (Nei 1978), unweighted pair group method (UPGM) projection of a matrix of these distances (Sneath and Sokal 1973), average heterozygosities, and the number of alleles per locus.

Results and discussion

Our analyses focused on a comparison of genetic characteristics between chinook salmon from the Klamath and Snake Rivers. Discussion of population structure within these two areas appears elsewhere, as do more

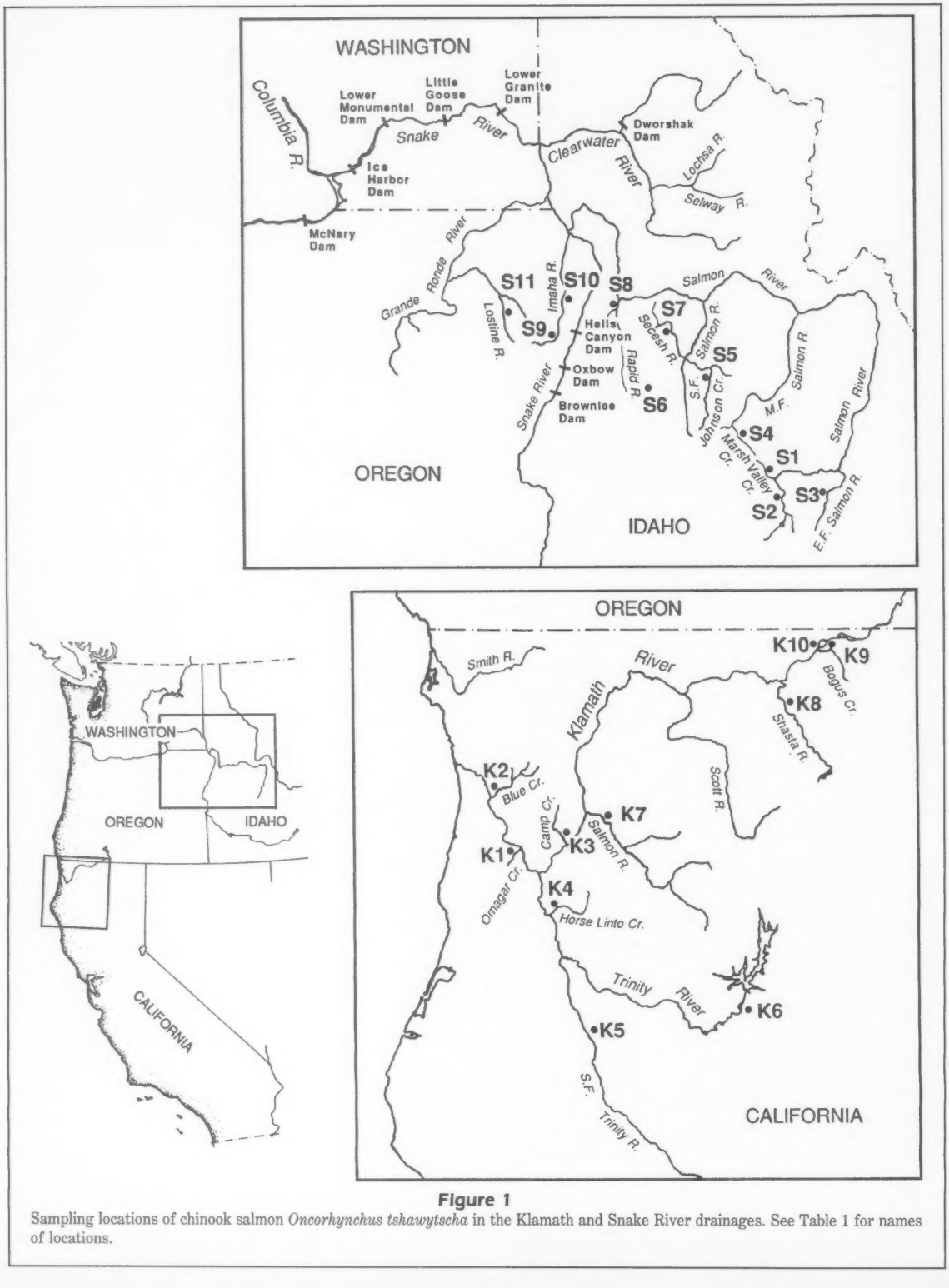


Figure 1

Sampling locations of chinook salmon *Oncorhynchus tshawytscha* in the Klamath and Snake River drainages. See Table 1 for names of locations.

Table 2

Enzymes and loci examined (enzyme nos. in parentheses) of chinook salmon *Oncorhynchus tshawytscha*.

Enzyme	Locus	Enzyme	Locus
Aspartate aminotransferase (2.6.1.1)	*sAAT-1,2**	Tripeptide aminopeptidase (3.4.11.4)	*PEPB-1**
	*sAAT-3**	Leucine-tyrosine dipeptidase (3.4.-.-)	*PEP-LT**
	*sAAT-4**	Malate dehydrogenase (1.1.1.37)	*sMDH-B1,2**
Adenosine deaminase (3.5.4.4)	*ADA-1**		*mMDH-1**
Alcohol dehydrogenase (1.1.1.1)	*ADH*4*		*mMDH-2**
Aconitate hydratase (4.2.1.3)	*sAH-1**	Malic enzyme (1.1.1.40)	*sMEP-1**
	*mAH-4**	Mannose-6-phosphate isomerase (5.3.1.8)	*MPI**
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	*GAPDH-3**	Phosphogluconate dehydrogenase (1.1.1.44)	*PGDH**
Dipeptidase (3.4.13.11)	*PEPA**	Phosphoglycerate kinase (2.7.2.3)	*PGK-2**
Glutathione reductase (16.4.2)	*GR**	Phosphoglucomutase (2.7.5.1)	*PGM-2**
Hydroxyacylglutathione hydrolase (3.1.2.6)	*HAGH**	L-Iditol dehydrogenase (1.1.1.14)	*IDDH-1**
Isocitrate dehydrogenase (1.1.1.42)	*sIDHP-1**	Superoxide dismutase (1.15.1.1)	*sSOD-1**
	*sIDHP-2**	Triose-phosphate isomerase (5.3.1.1)	*TPI-4**
Lactate dehydrogenase (1.1.1.27)	*LDH-B2**		
	*LDH-C**		

Table 3

Range of common allele frequencies in samples of chinook salmon *Oncorhynchus tshawytscha* from the Snake and Klamath Rivers reported in three investigations. Parenthetical entries summarize data from studies (2) and (3), respectively, for those populations studied in (1). Subset (A) are loci common to all studies; subset (B) are isolocus pairs unique to study (1); subset (C) are loci newly resolved in studies (2) and (3).

		(1) Utter et al. 1989		(2) Waples et al. 1991	(3) Bartley et al. 1992	
	Locus	Snake	Klamath	Snake	Klamath	
(A)	*sAAT-1,2**	0.981–1.000	0.995–1.000	0.957–1.000 (0.957–1.000)	1.000	(1.000)
	*sAAT-3**	0.994–1.000	0.995–1.000	0.965–1.000 (0.980–1.000)	0.985–1.000	(0.985–1.000)
	*ADA-1**	0.953–0.969	1.000	0.846–1.000 (0.894–1.000)	0.995–1.000	(1.000)
	*sAH-1**	0.994–1.000	0.995–1.000	0.985–1.000 (0.990–1.000)	0.940–1.000	(0.940–1.000)
	*PEPA**	0.994–1.000	0.990–1.000	0.995–1.000 (0.995–1.000)	0.770–1.000	(0.930–1.000)
	*GR**	1.000	0.995–1.000	0.995–1.000 (0.985–1.000)	0.995–1.000	(1.000)
	*LDH-B2**	0.972–1.000	1.000	0.970–1.000 (0.970–0.995)	1.000	(1.000)
	*LDH-C**	0.976–1.000	1.000	0.920–1.000 (0.920–1.000)	0.890–1.000	(0.980–1.000)
	*PEPB-1**	0.944–0.976	0.949–0.990	0.904–0.985 (0.904–0.985)	0.860–1.000	(0.980–1.000)
	*sMDHB-1,2**	0.995–0.998	0.997–1.000	0.942–0.997 (0.944–0.990)	0.993–1.000	(0.997–1.000)
	*MPI**	0.910–0.953	0.975–0.990	0.770–0.990 (0.884–0.990)	0.860–1.000	(0.970–0.992)
	*PGK-2**	0.062–0.139	0.146–0.350	0.065–0.187 (0.065–0.187)	0.148–0.400	(0.148–0.320)
	*sSOD-1**	0.944–0.976	0.895–0.990	0.885–0.980 (0.939–0.980)	0.755–0.992	(0.845–0.992)
(B)	*sIDHP-1,2**	0.913–0.937	1.000	—	—	
	*PGM-1,2**	1.000	0.942–0.990	—	—	
(C)	*TPI-4**	—	—	0.825–0.955	0.995–1.000	
	*sAAT-4**	—	—	0.919–1.000	0.985–1.000	
	*ADH**	—	—	0.985–1.000	1.000	
	*mAH-4**	—	—	0.985–1.000	0.775–1.000	
	*GAPDH-3**	—	—	1.000	0.871–1.000†	
	*HAGH**	—	—	0.902–1.000	1.000	
	*sIDHP-1**	—	—	0.783–0.950	0.992–1.000	
	*sIDHP-2**	—	—	0.945–1.000	0.900–1.000	
	*PEP-LT**	—	—	0.870–0.985	0.985–1.000	
	*mMDH-1**	—	—	0.995–1.000	0.795–1.000	
	*mMDH-2**	—	—	0.490–0.800	0.905–1.000	
	*sMEP-1**	—	—	0.010–0.079	0.150–0.465	
	*PGDH**	—	—	1.000	0.910–1.000	
	*PGM-2**	—	—	1.000	0.860–1.000	
	*IDDH-1**	—	—	0.897–1.000	0.990–1.000	

†Data from Gall et al. 1989

complete details of the individual studies. (Bartley et al. 1992, Waples et al. 1991).

Variability within populations

The levels of genetic variation within populations were evaluated using only the loci found to be polymorphic. Because this restriction does not represent a random sample of gene loci, values reported here are applicable only for comparisons among populations included in this study or with other studies using the same set of loci. Indices of genetic variability were consistently slightly higher in the Snake River samples; the average number of alleles per locus was 1.63 vs. 1.51 for the Klamath River, and the average heterozygosity was 0.079 vs. 0.065 ($0.05>p>0.01$ in both instances, based on Mann-Whitney tests). Heterozygosities ranged from 0.058 to 0.090 in the Snake River populations and were less uniform in the Klamath River groups, where both the lowest (0.039 in Shasta River) and the highest (0.126 in Omagar Creek) values were found. Neither of these latter two populations were represented in the initial study of the Klamath River by Utter et al. (1989). The actual heterozygosity values reported here are higher than those reported by Utter et al. (1989), primarily because a number of new, very polymorphic systems are included in the more recent analyses. Nevertheless, Utter et al. (1989) also found a slightly higher average heterozygosity in Snake River spring-run and summer-run chinook salmon (0.035–0.045) than in those from the Klamath River (0.027–0.032). Based on the new data, Waples et al. (1991) concluded that, in comparison with other Columbia River populations, Snake River spring-run and summer-run chinook salmon have somewhat reduced levels of genetic variability, but that the difference is apparently not as large as suggested by earlier studies (Utter et al. 1989, Winans 1989).

Variability between regions

Allele frequency distributions differed substantially between the two regions at a number of gene loci. Although three or more alleles were found at some of these loci, most of the important differences were reflected in differing frequencies of the common allele (Table 3). Particularly large differences were found at *mMDH-2** and *sMEP-1** (Fig. 2); for these loci, the range of allele frequencies was nonoverlapping between regions, with substantially higher frequencies of the common (i.e., *100**) allele found in the Klamath River samples at both loci.

Genetic differences between the two regions based on data for all 30 loci are summarized in a phenogram resulting from clustering of pairwise genetic distances (Fig. 3). The Snake and Klamath River populations are separated by a mean genetic distance of 0.014, whereas the within-river separations average 0.004 and 0.007,

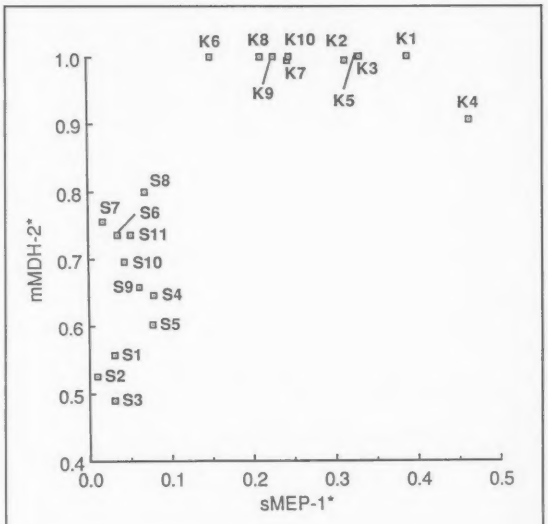


Figure 2
Plot of frequencies of common alleles of Klamath (K) and Snake (S) River populations of chinook salmon *Oncorhynchus tshawytscha* at the *mMDH-2** and *sMEP-1** loci.

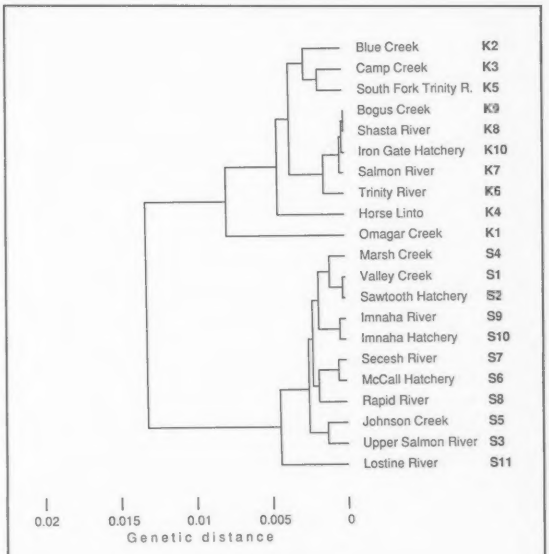


Figure 3
UPGM projection of Nei's genetic distances between Klamath and Snake River populations of chinook salmon *Oncorhynchus tshawytscha*.

respectively. The present data, then, clearly identify two genetically-distinct groups on the basis of the 30 polymorphic loci that were examined.

This genetic distinction clearly rejects a hypothesis of a recent common ancestry for populations of these regions. The topography of the clustering within Klamath and Snake River groups and the relative genetic distance between them are very similar to those distinguishing Klamath River populations from other genetically-distinct population groups of California and the Oregon Coast based on a similar set of polymorphic loci (Bartley et al. 1992).

Comparison with previous information

Because the clear separation of Snake and Klamath River populations reported here contrasts sharply with the minimal differences detected between these groups by Utter et al. (1989), an examination of results from that earlier study is warranted. A direct comparison of the original study with the two more recent studies is complicated by (1) the addition of a number of new gene loci in the more recent studies, (2) the greater discriminatory capabilities for some loci used in the newer studies, and (3) the more extensive sampling of populations in the newer studies. A comparison of the 15 loci common to both the original and more recent studies was made for the five Snake River sampling sites (S1, S2, S5, S6, S8) and two Klamath River sites (K6, K10) that were sampled in both investigations. In general, very similar allele frequencies were found at most loci in the two sets of samples (Table 3). None of the allele frequency differences between the original and the more recent studies exceeded 0.06 (at *PEPA** in the Klamath River comparisons). Thus, the more recent samples confirm the minimal differences between the two regions reported by Utter et al. (1989) based on the loci and populations originally examined.

The improved resolution in the more recent studies, therefore, can be attributed to an increase in the number and type of usable genetic characters. Particularly important was the addition of 15 gene loci not included in the earlier study (Table 3). Although regional differences are strongest at *mMDH-2** and *sMEP-1**, clear contrasts between the regions are also seen at five other loci (*mAH-4**, *GAPDH-3**, *HAGH**, *PEP-LT**, and *TPI-4**). In addition, the more recent studies resolve individual loci that had previously been considered isolocus pairs, which further enhanced the discriminating power of two genetic systems. This effect was most apparent for the enzyme IDH. Utter et al. (1989), as have other previous studies (e.g., Utter et al. 1987), reported variation for the isolocus pair *sIDHP-1,2**; subsequently, Shaklee et al. (1990) showed that it is possible to resolve the two loci individually. Whereas the most extreme frequency difference between the two regions at *sIDHP-1,2** was 0.087 (1.0–0.913; Table 3) in the original study, the maximum difference at *sIDHP-1** in the newer studies was 0.217 (1.0–0.783). Similarly, the protocol of Gall et al. (1989) for partitioning variation at the *PGM-1,2** isolocus increased the discriminatory power of this genetic system.

General implications of the results

During the 1960s, the newly found capability to resolve numerous genetic systems exhibiting Mendelian inheritance led to a flood of studies that continues to this day (see Lewontin 1991). Protein electrophoresis has been used extensively in fishery research and management (Utter 1991); such data have proven particularly useful in modifying previously held assumptions about the genetic structure of fish species (Allendorf et al. 1987). The results discussed here are instructive with regard to both the power and the limitations of such information.

The power of Mendelian data lies in the identification of genetic differences among individuals, populations and species. The regional differences among populations of North American chinook salmon originally described by Utter et al. (1989) have also been apparent in subsequent studies (Bartley and Gall 1990, Waples et al. 1991, Bartley et al. 1992). These differences have generally been interpreted to reflect more recent ancestries of populations within a particular genetically-defined region than between populations of different regions.

However, in spite of the power of electrophoretic data to detect genetic differences when present, there are limits to the conclusions that one can draw from the failure to detect such differences. That is, although a finding of a statistically-significant allele frequency difference may provide evidence that gene flow is restricted (or that some other evolutionary force is operating), the inability to identify such differences does not prove that genetic differences do not exist. The present example, in which genetically divergent groups were not well distinguished in a previous study, emphasizes the potential significance of this limitation. Although Utter et al. (1989) hypothesized that the apparent similarity between Klamath and Snake River chinook salmon was a coincidence that did not reflect a common ancestral origin, the distinctness of the two groups could not be demonstrated until new data became available. The situation is analogous to a classical genetic comparison between populations of *Drosophila pseudoobscura* from Berkeley, California and Bogata, Colombia, in which an initial apparent genetic similarity was puzzling in view of the exten-

sive geographic separation of the two regions (Lewontin and Hubby 1966). A subsequent study that found previously-unknown genetic variants (Singh et al. 1976) demonstrated clear genetic differences between populations of each region.

The important message here is to beware of the danger of drawing positive conclusions from negative data. It should also be emphasized that problems of this nature are not confined to genetic data; rather, the limitations of nondiscriminatory information (i.e., the power to reject the null hypothesis) should be considered in evaluating any kind of comparative data for two or more samples.

Similar allele frequencies among samples, then, support but do not confirm hypotheses that the samples are drawn from a common breeding group. This well-established principle requires restatement from time to time (e.g., Utter 1981, Waples 1991). Such awareness serves to safeguard against a premature conclusion of identity for groups that are distinct and thus may be subject to different management criteria.

In these instances it is important to recognize the power of Mendelian data involving multiple polymorphic loci to detect differences between populations when they do exist. For example, assuming that most allozyme variation is neutral, it will take populations that are divided into large units a considerable amount of time before significant divergence will occur. Thus, Atlantic herring *Clupea harengus* populations of the eastern and western Atlantic Ocean that have likely been isolated for thousands of years could not be distinguished because of similar allele frequencies at a number of polymorphic loci (Grant 1984). The observed value for Wright's (1943) fixation index (F_{st}) of 0.0042 approximates an F_{st} value of 0.003 expected for neutral markers among populations of effective size of 1 million individuals separated over 3000 generations (Nei and Chakravarti 1977). Such dynamics preclude genetic distinction of these herring populations through neutral genetic markers (and thus rejection of the null hypothesis) even with very large samples of loci and individuals. Under such circumstances, other criteria (e.g., tagging data) are needed to determine whether one or more populations is being sampled.

Finally, we note the complementary nature of relationships among populations indicated by many phenotypic traits on one hand and by most molecular genetic markers on the other hand. A strong selective component appears to be involved in the maintenance of phenotypic traits such as timings of spawning and migration (e.g., Ricker 1972, Helle 1981); consequently, relationships inferred from such traits tend to reflect relative similarities in adaptations among populations. Conversely, the apparent absence of strong selection at most electrophoretically detectable loci permits the estimation of relative degrees of gene flow within and among regions (e.g., Chakraborty et al. 1978, Allendorf and Phelps 1981), and such estimations provide useful insights about ancestral relationships. In view of the complementary nature of these different categories of genetic information, adequate sets of both molecular markers (for clarifying ancestral relationships) and phenotypic traits (for identifying adaptive differences within lineages) should be included in genetic surveys of a particular species whenever possible. Such adaptive differences have been noted within a number of apparent ancestral groupings of chinook salmon, including both spring- and fall-spawning migrations within the Klamath River populations of the species (Utter et al. 1989).

Acknowledgments

Research funded in part through contract DE-AI79-89BP0091 with Bonneville Power Administration.

Citations

Aebersold, P., G. Winans, D. Teel, G. Milner, and F. Utter
1987 Manual for starch gel electrophoresis: A method for the detection of genetic variation. NOAA Tech. Rep. NMFS 61, 19 p.

Allendorf, F., and S. Phelps
1981 Use of allelic frequencies to describe population structure. Can. J. Fish. Aquat. Sci. 38:1507–1514.

Allendorf, F., and G. Thorgaard
1984 Tetraploidy and the evolution of salmonid fishes. *In* Turner, B (ed.), Evolutionary genetics of fishes, p. 1–53. Plenum Press, NY.

Allendorf, F., N. Ryman, and F. Utter
1987 Genetics and fishery management: Past, present, and future. *In* Ryman, N., and F. Utter (eds.), Population genetics and fishery management, p. 1–20. Wash. Sea Grant Prog., Univ. Wash. Press, Seattle.

Bartley, D., and G. Gall
1990 Genetic structure and gene flow in chinook salmon populations of California. Trans. Am. Fish. Soc. 119:55–71.

Bartley, D., B. Bentley, J. Brodziak, R. Gomulkiewicz, M. Mangel, and G.A.E. Gall
1992 Geographic variation in population genetic structure of chinook salmon from California and Oregon. Fish. Bull., U.S. 90:77–100 (authorship amended per errata, Fish. Bull. 90(3):iii).

Chakraborty, R., P. Fuerst, and M. Nei
1978 Statistical studies on protein polymorphism in natural populations: II. Gene differentiation between populations. Genetics 88:367–390.

Gall, G.A.E., B. Bentley, C. Panattoni, E. Childs, C. Qi, S. Fox, M. Mangel, J. Brodziak, and R. Gomulkiewicz
1989 Chinook mixed fishery project 1986–1989. Report of the Department of Animal Science and the Department of Applied Mathematics, Univ. Calif., Davis, under Interagency Agreement C-1335 with Calif. Dep. Fish & Game, 192 p.

Grant, W.
1984 Biochemical population genetics of Atlantic herring. Copeia 1984:357–364.

Helle, J.
1981 Significance of the stock concept in artificial propagation of salmonids in Alaska. Can. J. Fish. Aquat. Sci. 38: 1665–1671.

Lewontin, R.
1991 Electrophoresis in the development of evolutionary genetics: Milestone or millstone? Genetics 128:657–662.

Lewontin, R., and J. Hubby
1966 A molecular approach to the study of genetic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura*. Genetics 54:595–609.

Nei, M.
1978 Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590.

Nei, M., and A. Chakravarti
1977 Drift variances of F_{st} and G_{st} statistics obtained from a finite number of isolated populations. Theor. Popul. Biol. 11:307–25.

Ricker, W.
1972 Hereditary and environmental factors affecting certain salmonid populations. *In* Simon, R., and P. Larkin (eds.), The stock problem in Pacific salmon, p. 19–161. H.R. MacMillan Lectures in Fisheries, Univ. Brit. Col., Vancouver.

Shaklee, J., and S. Phelps
1990 Operation of a large-scale, multiagency program for genetic stock identificiation. *In* Parker, N.C., et al. (eds.), Fish marking techniques, p. 817–830. Am. Fish. Soc. Symp. 7, Bethesda.

Shaklee, J., and C. Tamaru
1981 Biochemical and morphological evolution of Hawaiian bonefishes (*Albula*). Syst. Zool. 30:125–146.

Shaklee, J., F. Allendorf, D. Morizot, and G. Whitt
1989 Genetic nomenclature for protein-coding loci in fish: Proposed guidelines. Trans. Am. Fish. Soc. 118:218–227.

Shaklee, J., C. Busack, A. Marshall, M. Miller, and S. Phelps
1990 The electrophoretic analysis of mixed-stock fisheries of Pacific salmon. *In* Ogita, Z.I., and C.L. Markert (eds.), Isozymes: Structure, function, and use in biology and medicine, p. 235–265. Wiley-Liss, NY.

Singh, R., R. Lewontin, and A. Felton
1976 Genetic heterogeneity within electromorphic alleles of xanthine dehydrogenase in *Drosophila pseudoobscura*. Genetics 84:609–629.

Sneath, P., and R. Sokal
1973 Numerical taxonomy. W.H. Freeman, San Francisco, 573 p.

Swofford, D., and R. Selander
1981 BIOSYS-1--A FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72:281–283.

Utter, F.
1981 Biological criteria for definition of species and distinct intraspecific populations of salmonids under the U.S. Endangered Species Act of 1973. Can. J. Fish. Aquat. Sci. 38: 1626–1635.
1991 Biochemical genetics and fishery management: An historical perspective. J. Fish. Biol. 39(Suppl. A):1–18.

Utter, F., D. Teel, G. Milner, and D. McIsaac
1987 Genetic estimates of stock compositions of 1983 chinook salmon, *Oncorhynchus tshawytscha*, harvest off the Washington coast and the Columbia River. Fish. Bull., U.S. 85:13–23.

Utter, F., G. Milner, G. Ståhl, and D. Teel
1989 Genetic population structure of chinook salmon in the Pacific Northwest. Fish. Bull., U.S. 87:238–264.

Waples, R.
1991 Pacific salmon and the definition of "species" under the Endangered Species Act. Mar. Fish. Rev. 53(3):11–22.

Waples, R., D. Teel, and P. Aebersold
1991 A genetic monitoring and evaluation program for supplemented populations of salmon and steelhead in the Snake River Basin. Annu. Rep. Res., Contract DE-A179-89BP00911, U.S. Dep. Energy, 50 p. (Avail. Bonneville Power Admin., P.O. Box 3621, Portland OR 97208.)

Winans, G.
1989 Genetic variability in chinook salmon stocks from the Columbia River Basin. N. Am. J. Fish. Manage. 9:47–52.

Wright, S.
1943 Isolation by distance. Genetics 28:114–138.

Differentiating *Paralithodes* larvae using telson spines: A tail of two species*

Gregory C. Jensen
Helle B. Andersen
David A. Armstrong
School of Fisheries WH-10, University of Washington, Seattle, Washington 98195

Identification of larvae belonging to closely related species of decapod Crustacea is frequently dependent upon few (often single) morphological characters. Since larvae used in descriptions are often the offspring from a single captive, very little is known about how intraspecific variability may affect the ability to differentiate species. Two congeneric decapods whose zoeae are separated on the basis of a single morphological character are the red king crab (RKC) *Paralithodes camtschaticus*, and blue king crab (BKC) *P. platypus*. Larvae of these commercially-important species are distinguished from each other by the number of spines or processes on the telson, RKC having 7 pairs of spines and BKC 8 pairs, excluding a minute seta (Sato 1958, Haynes 1984). However, when viewed together there are other apparent differences: BKC zoeae have proportionately shorter rostrums and carapace spines, larger bodies at each stage, and larger eyes.

During the course of extensive plankton sampling for king crab larvae in Herendeen Bay within Port Moller, Alaska, considerable variability in telson morphology was noted. A large proportion of zoeae resembling BKC were captured having an asymmetrical pattern of 8+7 telson spines, while others, also appearing to be BKC in other respects, had only 7 pairs; such interspecific character overlap had not been noted with these two species near the Pribilof Islands, Alaska (Armstrong et al. 1985). To confirm the identity of these zoeae and provide additional characters to separate the two species, several measurements were taken on specimens from Herendeen Bay and the Pribilof Islands to establish a stronger, more quantitative basis to distinguish these larvae.

* Contribution 867 of the School of Fisheries, University of Washington.

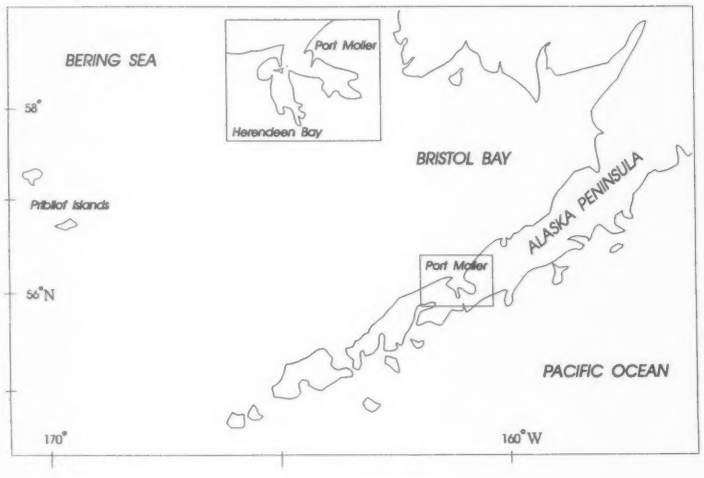


Figure 1
Locations of *Paralithodes* spp. zoeae collections.

Materials and methods

Paralithodes zoeae were collected near the Pribilof Islands, Alaska, in May 1983 and April 1984, and from Herendeen Bay, Alaska (Fig. 1) in May and June of 1990, using either a 505 μm mesh Tucker trawl or a 60 cm bongo net with a mesh of 333 or 505 μm. Samples were preserved in 5% buffered formalin in seawater and later sorted for target species, which were transferred to a solution of 70% ethanol and 5% glycerol. The number of telson spines (excluding a minute seta) was recorded for each specimen, and three measurements were taken: tip of rostrum to the anteriormost edge of the eye ("rostrum length"), anterior edge of eye to the tip of the posteriolateral carapace spines ("carapace length"), and the longest dimension of the eye ("eye length," Fig. 2). Damaged or distorted specimens were not used for measurements, but spine counts were recorded. A total of 608 larvae were measured; 371 from Herendeen Bay and the remainder from around the Pribilof Islands. The ratios of rostrum length to carapace length were plotted against carapace length for "normal" (i.e., 7+7 telson spine RKC and 8+8 BKC)

Manuscript accepted 1 July 1992.
Fishery Bulletin, U.S. 90:778–783 (1992).

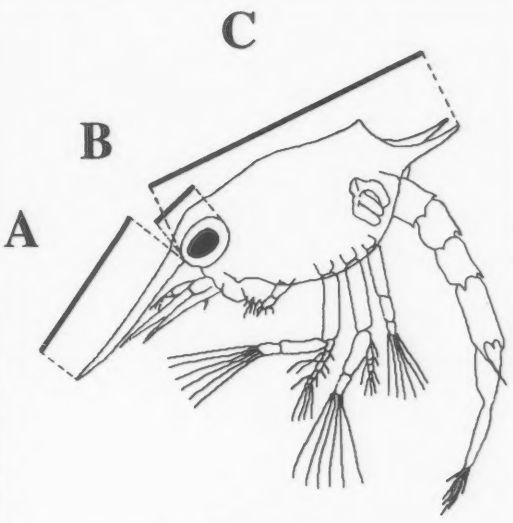


Figure 2
Measurements taken from *Paralithodes* spp. zoeae. (A) rostrum length, (B) eye length, (C) carapace length.

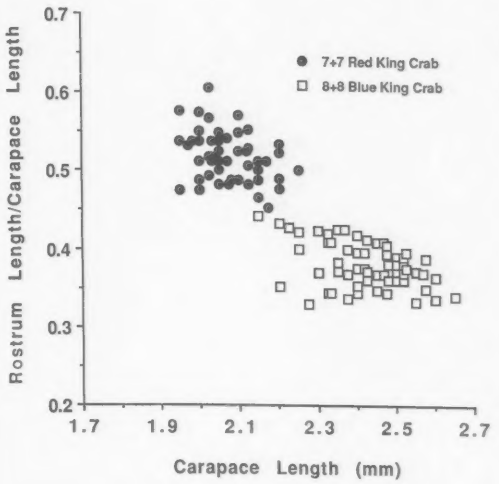


Figure 3
Ratios of rostrum length/carapace length for first-stage *Paralithodes* spp. collected near the Pribilof Islands, Alaska.

zoeae of both species in the two areas. Those with an anomalous number of spines (8+7 and "BKC" with 7+7) were then similarly plotted for comparison.

Unless otherwise indicated, data are presented as mean ±1 standard deviation. ANOVAs were used to test for significant differences ($\alpha \leq 0.05$) between the means of different groups, and the means compared using Tukey's T method. A two-way ANOVA was used to examine intraspecific variation in zoeae I between the two areas.

Results

Plotted ratios of rostrum length/carapace length for Pribilof Island specimens fell into two distinct clouds representing those thought to be RKC (longer rostrum) and BKC (Fig. 3). These were not so clearly separated in the samples from Herendeen Bay; nevertheless, all those with an asymmetric telson spine pattern or a short rostrum, large body, and spine count of 7+7 fell within the cloud of 8+8 BKC larvae (Fig. 4). These larvae were designated as BKC and divided into groups based on number of telson spines. The ratios for all of these groups were significantly different ($p<0.05$) at each zoeal stage from the means for RKC zoeae; Figure 5 shows combined results for both species at the two locations. Both the carapace and eyes of BKC larvae were significantly longer than those of RKC at all

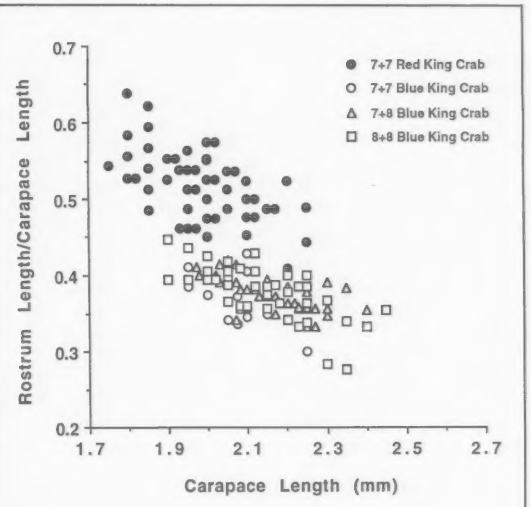


Figure 4
Ratios of rostrum length/carapace length for first-stage *Paralithodes* spp. zoeae collected from Herendeen Bay, Alaska.

stages, but these differed considerably between the two areas. Two-way ANOVA revealed no significant difference in rostrum/carapace length ratio for zoeae-I BKC from the two areas, but significantly smaller

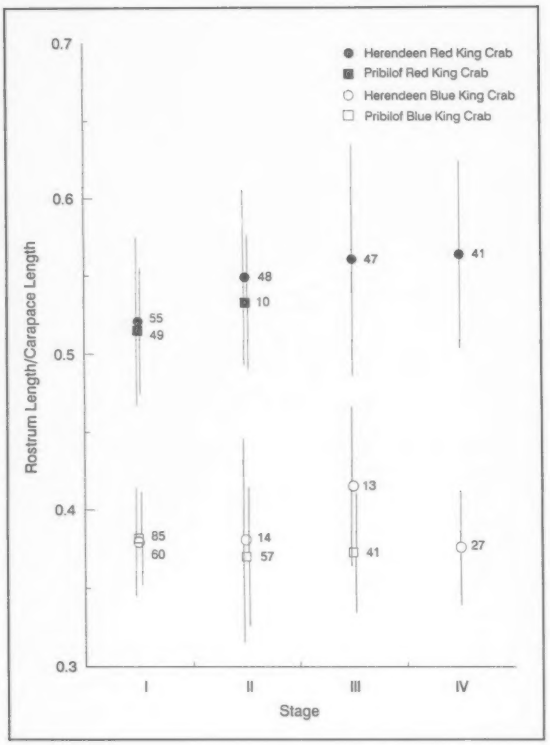


Figure 5
Paralithodes spp. rostrum length/carapace length by stage. Values are mean ratios (±1 SD); numbers are the number of zoeae measured for each value.

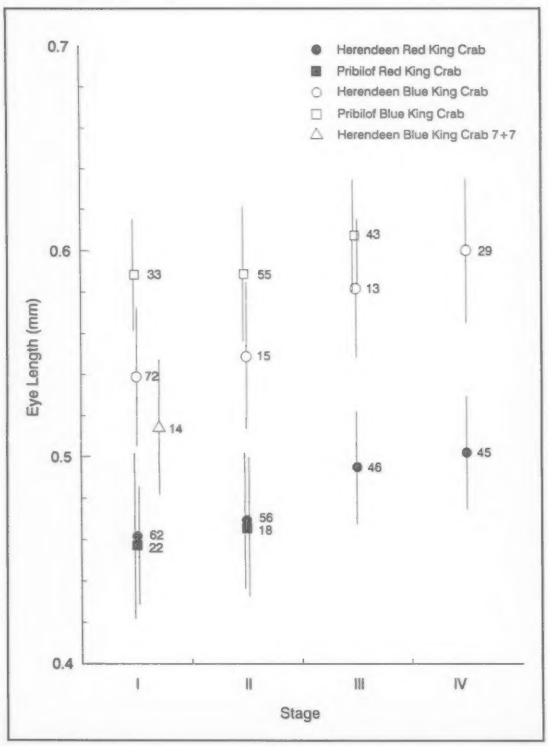


Figure 6
Mean eye length (±1 SD), and number of *Paralithodes* spp. zoeae measured.

eyes for Herendeen Bay BKC, suggesting that eye length is not reliable for distinguishing the two species. No intraspecific differences between areas were detected for either rostrum/carapace length or eye length for RKC.

The mean eye length of RKC larvae was significantly less ($p<0.05$) at each stage than the means of all groupings of BKC. In addition, the mean of the 7+7 zoeae-I BKC was significantly less than those with 8+8 (Fig. 6). BKC larvae from Herendeen Bay showed great variation in number of telson spines. Only 45.9% of all BKC larvae had a spine count of 8+8, the majority having some other combination of 7, 8, or 9 spines on each side of the telson. In contrast, the majority of BKC zoeae from the Pribilof Islands (84%) had a spine count of 8+8 (Fig. 7). RKC larvae showed little variation in telson spines, with only 0.9% of the zoeae from Herendeen Bay and 3.2% from the Pribilof Islands deviating from the count of 7+7.

Discussion

BKC zoeae are generally distinguished from RKC zoeae by the presence of an additional pair of inner spines on the telson (Fig. 8A,B), and for king crab zoeae collected near the Pribilof Islands this was a reliable character for separating the two species. Only 3.2% of the RKC zoeae collected from this area deviated from the 7+7 pattern. Even though 16% of the BKC zoeae differed from 8+8, this difference was almost invariably in the form of an extra 1 or 2 inner spines, making confusion with RKC unlikely. BKC zoeae were visibly much larger as confirmed by their greater carapace length, and had shorter rostrums and larger eyes.

A substantially different pattern was apparent in samples from Herendeen Bay, where 42% of zoeae-I BKC were missing one spine from the telson (Fig. 8C) and an additional 18% missing two spines (Fig. 8D). Because the missing spines are the innermost of the two pairs, those remaining tend to be considerably longer than the single pair in RKC; yet as Figure 8D

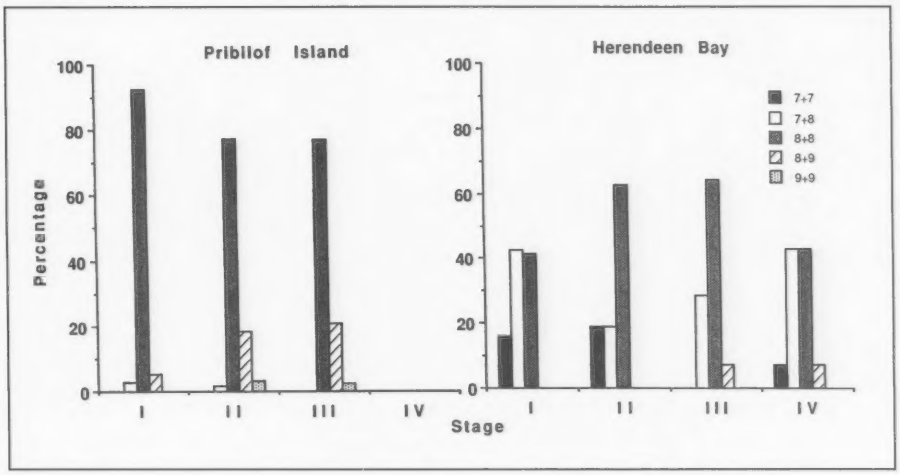


Figure 7
Number of telson spines of *Paralithodes platypus* zoeae collected from the Pribilof Islands and Herendeen Bay.

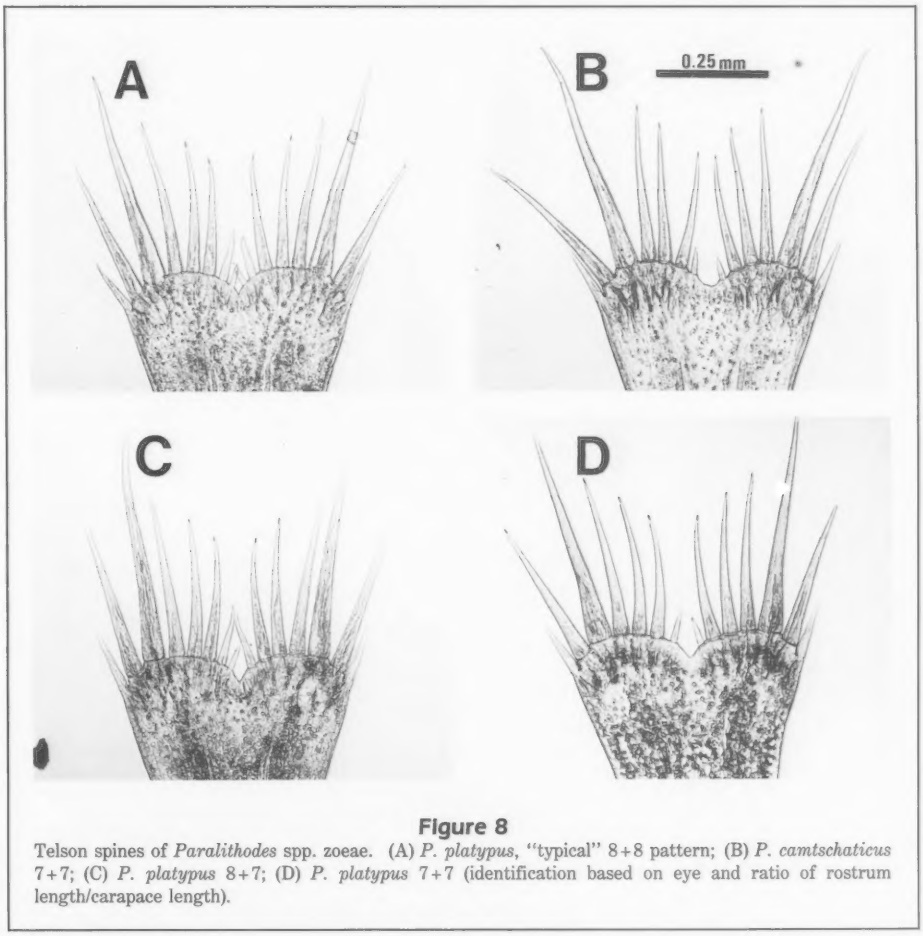


Figure 8
Telson spines of *Paralithodes* spp. zoeae. (A) *P. platypus*, "typical" 8+8 pattern; (B) *P. camtschaticus* 7+7; (C) *P. platypus* 8+7; (D) *P. platypus* 7+7 (identification based on eye and ratio of rostrum length/carapace length).

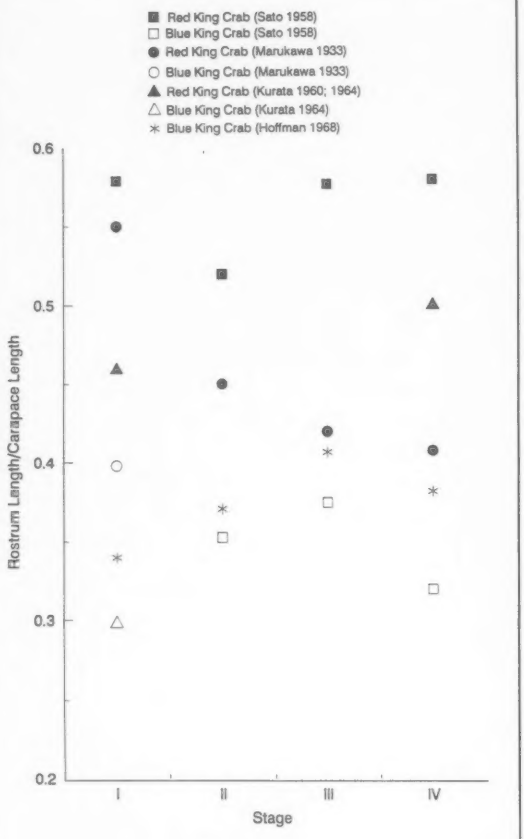


Figure 9
Rostrum/carapace length ratios of *Paralithodes* spp. zoeae taken from published illustrations.

shows, this difference is sometimes negligible. However, BKC were readily distinguished from RKC by their proportionately shorter rostrums, larger eyes, and larger bodies, but the differences were not as great as those seen in the Pribilof Islands. Zoeae in both locations appeared to gain additional telson spines with larval stage, a pattern noted previously for other lithodid larvae by Kurata (1964). While rostrum length alone was not reliable for separating the two species (due to intraspecific variation between the two areas), the proportion of rostrum length to carapace length remained constant and appears to be a useful method of differentiating the two. Whether this is reliable in other areas is not known, but it is consistent with illustrations in published descriptions of the two species (Fig. 9).

Of particular interest is the intraspecific variability exhibited both between the two areas and within the population in Herendeen Bay. While there were no significant differences between populations of RKC, all linear measurements of BKC zoeae from Herendeen Bay averaged 10–12% smaller than those of conspecifics from the Pribilof Islands. The cause of this variation is not known, but environmental factors such as temperature can affect both the number of decapod larval stages (Knowlton 1974) and their morphology (Shirley et al. 1987). Temperatures differed considerably between the two areas at the time of larval collection. At the Pribilof Islands in May 1983 the water was 2–4°C, and −1–1.5°C in April 1984 (Armstrong et al. 1985). In Herendeen Bay larvae stayed above a 40 m thermocline in water 2.5–8.5°C, and developmental times were exceptionally fast (Wainwright et al. 1991).

BKC have an extremely disjunct distribution (Somerton 1985), and it is also possible that size differences could be related to their reproductive isolation. But although local environmental features or isolation may explain differences between the two populations, they are unlikely to account for the variation seen within the relatively small scale of Herendeen Bay. The eyes of BKC zoeae having a 7+7 spine pattern were intermediate in length between the 8+8 or 8+7 BKC larvae and RKC from Herendeen Bay (Fig. 7). The cause of such differences cannot be known without appropriate experiments and genetic studies, but the recent report of an adult RKC-BKC hybrid from the Sea of Okhotsk (Nizyayev 1991) raises the possibility that some interbreeding may occur within the confines of Herendeen Bay.

Because all larvae were collected from the plankton rather than hatched in captivity, we cannot state unequivocally that these differences in spine count are due to intraspecific variation of BKC rather than a mixture of other lithodid species. However, megalopae, juveniles, and adults of RKC and BKC were collected within Herendeen Bay during the course of this study; despite extensive trawling, pot fishing, dredging, and intertidal surveys, the only other lithodid found was *Hapalogaster grebnitzkii*. Larvae matching the description for *H. grebnitzkii* were also the only other lithodid zoeae occurring in the plankton samples. The large size, shape, and position of the posterolateral carapace spines, coupled with a lack of carapace sculpturing, readily distinguish RKC and BKC zoeae from other described species of Bering Sea lithodids. We believe it is extremely unlikely that the variation is due to a fourth, undescribed species.

No single character for reliably separating BKC and RKC zoeae was observed, but since the number of telson spines is useful for differentiating the two species in some areas (e.g., Pribilof Islands), we suggest using this count along with the rostrum/carapace

length ratio until the extent of character overlap is known. A ratio of >0.45 (RKC) or <0.45 (BKC) usually distinguished the species in our samples from both areas. Eye measurements, like spine counts, vary with area but can be useful when the rostrum or carapace is damaged or distorted. In our samples the overlap in telson spine counts was greatest in zoeaeI, but fortunately this was the stage when the two species could be most reliably distinguished by the proportion of rostrum to carapace length.

Acknowledgments

We thank Mike McGurk and Dave Warburton of Triton, Ltd., for their help in the field, and Trent McDonald, Pam Wardrup, and Tom Wainwright for suggestions and advice. This study was funded by Minerals Management Service of the Department of the Interior, through an interagency agreement with the National Oceanic and Atmospheric Administration, Department of Commerce, as part of the Alaska Outer Continental Shelf Environmental Assessment Program (OCSEAP).

Citations

Armstrong, D.A., J.L. Armstrong, R. Palacios, G. Williams, G.C. Jensen, and W. Pearson
1985 Early life history of juvenile blue king crab, *Paralithodes platypus*, around the Pribilof Islands. *In* Melteff, B.R. (ed.), Proceedings of the international king crab symposium, p. 211–229. Rep. 85-12, Univ. Alaska Sea Grant Prog., Fairbanks.

Haynes, E.B.
1984 Early zoeal stages of *Placetron wosnessenskii* and *Rhinolithodes wosnessenskii* (Decapoda, Anomura, Lithodidae) and review of lithodid larvae of the northern North Pacific Ocean. Fish. Bull., U.S. 82:315–324.

Hoffman, E.G.
1968 Description of laboratory-reared larvae of *Paralithodes platypus* (Decapoda, Anomura, Lithodidae). J. Fish. Res. Board Can. 25:439–455.

Knowlton, R.E.
1974 Larval developmental processes and controlling factors in decapod Crustacea, with emphasis on Caridea. Thalassia Jugosl. 10:138–158.

Kurata, H.
1960 Last stage zoea of *Paralithodes* with intermediate form between normal last stage zoea and glaucothoe. Bull. Hokkaido Reg. Fish. Res. Lab. 22:49–56 [in Jpn., Engl. synop.].
1964 Larvae of decapod Crustacea of Hokkaido. 6. Lithodidae (Anomura). Bull. Hokkaido Reg. Fish. Res. Lab. 29:49–65 [in Jpn., Engl. summ.].

Marukawa, H.
1933 Biological and fishery research on Japanese king-crab *Paralithodes camtschatica* (Tilesius). J. Imp. Fish. Exp. Stn. 4, 152 p. [in Jpn., Engl. abstr.].

Nizyayev, S.A.
1991 Finding of a hybrid crab specimen with the characters of *Paralithodes camtschatica* and *P. platypus* in the Sea of Okhotsk. Zool. Zh. 9:128–131 [in Russ., Engl. summ.].

Sato, S.
1958 Studies on larval development and fishery biology of king crab, *Paralithodes camtschatica* (Tilesius). Bull. Hokkaido Reg. Fish. Res. Lab. 17:1–102 + plates [in Jpn., Engl. summ.].

Shirley, S.M., T.C. Shirley, and S.D. Rice
1987 Latitudinal variation in the Dungeness crab, *Cancer magister*: Zoeal morphology explained by incubation temperature. Mar. Biol. (Berl.) 95:371–376.

Somerton, D.A.
1985 The disjunct distribution of blue king crab, *Paralithodes platypus*, in Alaska: Some hypotheses. *In* Melteff, B.R. (ed.), Proceedings of the international king crab symposium, p. 13–21. Rep. 85-12, Univ. Alaska Sea Grant Prog., Fairbanks.

Wainwright, T.C., D.A. Armstrong, H.B. Andersen, P.A. Dinnel, D.W. Herren, G.C. Jensen, J.M. Orensanz, and J.A. Shaffer
1991 Port Moller king crab studies: Annual report. Fish. Res. Inst. Rep. FRI-UW-9203, Univ. Wash., Seattle, 38 p.

A telemetric study of the home ranges and homing routes of lingcod *Ophiodon elongatus* on shallow rocky reefs off Vancouver Island, British Columbia

Kathleen R. Matthews

Pacific Southwest Research Station, U.S. Forest Service
Box 245, Berkeley, California 94701

Lingcod *Ophiodon elongatus* are an important commercial and recreational fish in the northeast Pacific (Miller and Geibel 1973, Cass et al. 1990). In some areas lingcod show serious population declines. In Washington, after signs of depletion, the fishery was closed in central Puget Sound for 5 years (1978–83) to allow rebuilding (Buckley et al. 1984). Currently in central Puget Sound, the now tightly-restricted fishery allows only recreational use, a 6-week opening, and a daily limit of 1 fish. Similarly in British Columbia, landings and average size of the catch have declined and tighter regulations imposed (Richards and Hand 1991). Because of lingcod declines, it is crucial to understand their life-history characteristics in order to determine possible causes of decline and to help recovery efforts. One area of uncertainty regarding lingcod life history is their movement behavior.

Despite a number of studies of lingcod movements (Miller and Geibel 1973, Mathews and La Riviere 1987, Jagielo 1990, Smith et al. 1990), many questions remain about their movement patterns. Most studies describe lingcod as sedentary (Miller and Geibel 1973, Mathews and La Riviere 1987, Smith et al. 1990); yet lingcod do make migrations, and movement up to 385km has been documented (Mathews and La Riviere 1987, Jagielo 1990). Although not verified through tagging, it is thought that most lingcod movements, including possible homing behavior, are related to spawning. Female lingcod may seasonally leave deeper reefs and move inshore to lay demersal eggs that the shallower living males guard. There is indirect evidence for the inshore movement of females; an increase of larger gravid females in the inshore catch occurs during fall months just prior to spawning (Miller and Geibel 1973).

Furthermore, some studies have indicated the homing behavior of lingcod, similar to many rocky reef fishes (Hart 1943, Williams 1957, Carlson and Haight 1972, Matthews 1990); i.e., when fish move away for any reason (including spawning, experimental displacement, etc.) they will return to areas previously occupied (Gerking 1959). In an early study in Canada, 4 of 14 displaced lingcod returned 9.7km to original capture sites (Hart 1943). Additional evidence of lingcod homing behavior came from an attempt to enhance overfished areas by transplanting lingcod (Buckley et al. 1984). None of the transplanted lingcod were resighted at the release area (i.e., the enhancement was unsuccessful), whereas nine of the transplanted lingcod were caught close to the original capture site (190km from release site).

Lingcod movement behavior has implications for enhancement efforts and habitat management. Attempts to rebuild populations in overfished areas by transplanting lingcod from areas of higher abundance would be unsuccessful if lingcod simply returned to their original home sites. Furthermore, movement information is valuable because if lingcod preferentially home to certain reefs, then those reefs could be designated as management reserves. Thus, any new knowledge of lingcod homing will lead to a better understanding of their movement behavior and the effect of rehabilitation efforts. The objectives of this pilot study were to use ultrasonic tagging to (1) describe home ranges and movements of lingcod on rocky reefs, and (2) determine the homing routes of displaced lingcod.

Methods

Study sites

The study was conducted during April 1990 off eastern Gabriola Island on the eastern side of Vancouver Island, British Columbia (Fig. 1). The area is characterized by extensive shallow rocky reefs and pinnacles. Depths encountered during ultrasonic tracking were in the range 3–35m. Two reef areas were chosen for the tracking work: Gabriola reefs and Valdes reefs (each is actually a series of small, separate reefs) (Fig. 1). Both reefs are approximately 15–30m deep, although shallower areas were sometimes encountered. Although bullkelp *Nereocystis leutkeana* is present on these reefs during the summer and fall, no surface kelp was present during this April study.

Ultrasonic tagging

The transmitters (48×15mm, 18g in air, 8.3g in seawater) were ex-

Manuscript accepted 29 July 1992.
Fishery Bulletin, U.S. 90:784–790 (1992).

ternally attached using methods used for tuna (Holland et al. 1985). The nylon loop on the transmitter anchored one inelastic pull tie, with another tie wrapped around the tag's opposite end. The two pull ties were inserted through the dorsal musculature and cinched down to prevent the transmitter from dangling.

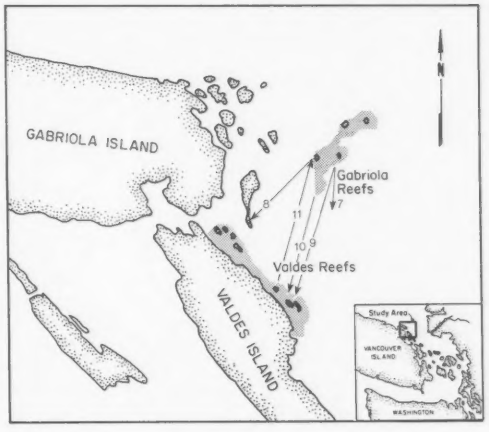


Figure 1
Map of study area and general displacement directions for *Ophiodon elongatus* fish nos. 7–11. Fish were captured and displaced in the direction shown by arrow.

Lingcod were captured on hook-and-line, placed in a seawater-filled cooler, and anesthetized (methomidate hydrochloride). After tags were attached, lingcod were allowed to recover in fresh (without anesthetic) seawater prior to release. Fish appeared completely recovered from the anesthetic and tagging procedure ~5–10 min after tagging.

Eleven transmitters with replaceable batteries (Vemco V3-1H-R pingers, Vemco Ltd., Nova Scotia, Canada B3L 4J4) were operated at five crystal-controlled frequencies: 50.0 (2 tags), 60.0 (2 tags), 65.54 (3 tags), 69.0 (2 tags), and 76.8 (2 tags) kHz, corresponding to pre-set channels on the Vemco VR-60 receiver. Tags assigned to the same channel were easily differentiated by their unique pulse period, which was automatically decoded and displayed by the receiver. To locate the transmitters, a Vemco V-10 directional hydrophone was employed from a small boat. Once a tag was located, the boat's position was determined, using LORAN-C readings, depth, and visual compass bearings of four charted features (buoys, lights, etc.), in the study area on an almost daily basis (one of 21 tracking days was missed due to boat breakdown) for the life of the transmitter (21 d battery life). One reason this study area was chosen was the presence of several flashing lights and buoys which made navigation and location determination easier, especially at night.

During 5–27 April 1990, 11 lingcod (57.0–80.6 cm total length, TL) were tagged and monitored (Table 1).

Table 1
Summary of total lengths and duration of tracking of lingcod *Ophiodon elongatus* equipped with ultrasonic transmitters in the Strait of Georgia, British Columbia, and monitored 5–27 April 1990 to measure home ranges and homing routes. Nocturnal movement occurred 24:00–06:00.

Tag no.	Sex	Length (TL cm)	Date tracking began	Duration (d)	Nondisplaced lingcod home ranges			
Controls								
1	Female	67.5	4/5/90	20	Captured and released at Valdes reefs			
2	Male	62.1	4/5/90	16	Captured and released at Valdes reefs			
3	Male	59.5	4/9/90	19	Captured and released at Valdes reefs			
4	Male	69.8	4/8/90	15	Captured and released at Gabriola reefs			
5	Female	80.6	4/9/90	12	Captured and released at Gabriola reefs			
6	Female	68.4	4/9/90	15	Captured and released at Gabriola reefs			
					Displaced lingcod homing routes			
					Distance moved (km)	Total time to return (h)	Movement rate (m/h)	Nocturnal movement rate (m/h)
Experimentals								
7	Male	66.2	4/12/90	14	1.0	40	25	83.3
8	Male	57.0	4/16/90	12	2.2	Did not return		
9	Male	64.0	4/19/90	9	2.8	60	48	233.3
10	Male	64.5	4/23/90	5	2.8	35	80	233.3
11	Male	69.5	4/25/90	3	2.8	33	85	233.3

Up to seven tagged fish were deployed within the study area at one time. One procedure was conducted on two rocky reefs to determine the home ranges of lingcod during the day, night, and periods of strong current which were predicted up to 14.8km/h (8.0kn) (Canadian tide and current tables, Canadian Hydrographic Service 1990). Six lingcod were captured, tagged, released, and monitored at the original point of capture, either Gabriola reefs area or Valdes reefs. Their geographic locations were determined on an almost daily basis (the only exception being 18 April) for the duration of the tag battery life.

To determine the homing routes of displaced lingcod, five males were captured, tagged, and displaced up to 2.8km in two opposite directions (Fig. 1). Four of the five displaced fish were moved south, while one fish was moved north. Because there was no information on the time required for lingcod to home, the first fish was moved a short distance (1km) to allow enough time to track its homeward movement. Of the remaining four lingcod, one was displaced 2.2km, and three were displaced 2.8km. The movements were then monitored almost continuously, with occasional rest breaks, until the transmitter batteries expired. Displaced fish were individually tracked because they required continuous monitoring. When the displaced fish were first released, an attempt was made to stay with the fish for several hours to detect any homeward movement.

The field schedule started with two teams each working 12h on the boat for a full 24h coverage. After the first few days of field work, we changed the schedule to devote our efforts to covering nighttime lingcod movement (16:00–08:00). The entire study covered 21 tracking days during 5–27 April (only 18 April was canceled due to boat problems) for a total of 336 tracking hours. When the nondisplaced fish were first released, an entire day was spent tracking those fish. Subsequently, each fish was periodically (about 15–20 times/tracking day) checked for its position, which allowed several tagged fish to be concurrently monitored. The five displaced fish were followed one at a time to ensure that their homing route could be detected.

On two separate dates, I conducted scuba observations to search for tagged lingcod and to collect information not available through telemetry. When a signal cannot be located, it was impossible to determine whether the tag battery has died or the fish has left the area; hence, I searched underwater for two tagged fish in their last recorded location after the signal could no longer be detected. Also, to determine the accuracy of telemetric locations, I used scuba observations to compare underwater positions of tagged fish with those provided by telemetry. Once the directional hydrophone positioned the boat directly over the tag's signal I then anchored the boat, descended, and searched for the tagged fish.

Results

Nondisplaced fish (controls)

The six lingcod (three females and three males) tagged and released at Gabriola and Valdes reefs were generally found close to release sites during the day, night, and periods of swift current. When relocated, the six lingcod were essentially in the same position (latitude–longitude differences were within 0.01–0.02 nmi, which is the normal resolution of the LORAN unit). Thus, there was no detectable difference in their home range size. Fish were monitored for 12–20d ($\bar{x}$ 16.2+2.9d) until the tag batteries expired.

These telemetry findings were verified by visual (scuba) resightings of two tagged lingcod. After determining the position of an ultrasonic tag, I later (within a few minutes) observed the tagged fish sitting on the bottom. These visual sightings also verified that the tags were still attached to the fish. Furthermore, after the signal had apparently died on two tagged fish, I searched underwater and saw the two tagged lingcod in their last recorded telemetry position.

The six individual lingcod were also monitored on six separate nights when the current ranged from slack to 10.4km/h (5.6kn) for a total of 50h of nighttime observation. Home ranges were similar to those observed in the day. However, signals were louder suggesting that the fish were out in the open, i.e., not under a rock (Matthews et al. 1990).

Displaced fish (experimentals)

The five displaced lingcod remained close to release sites and did not move for several hours following release (Figs. 2–6). These first few hours (both during the day and night) following release may be a recovery period in response to capture, handling, and tagging. Subsequently, four of the five displaced fish moved back to the capture site. Each fish had returned to the capture site by the end of the second night following release. Return trips were confined to the immediate vicinity of the Gabriola and Valdes Islands study area.

The four homing lingcod (nos. 7, 9–11) remained near the release site for 4–6h and returned to home sites in 33–60h (Figs. 2–5). These four fish started their homeward movements at night (20:30–06:00), and movement terminated once it became light at ~06:00.

No clear pattern was detected in the homeward movement, as lingcod did not appear to follow obvious features such as depth contours or currents. Homing lingcod traversed depths of 5–35m. Occasionally the

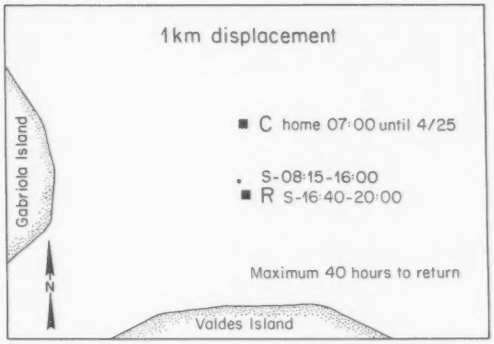


Figure 2
Positions of *Ophiodon elongatus* fish no. 7 (66.2 cm male) captured from site C, moved 1 km south to release site R, and monitored 12–25 April. S = stationary.

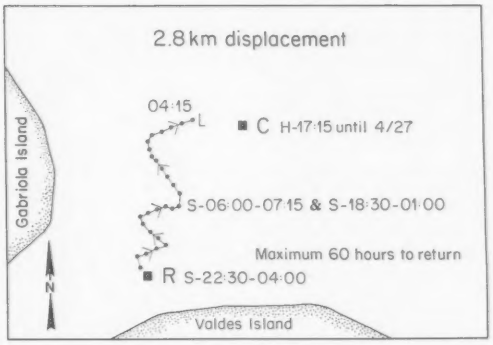


Figure 3
Positions of *Ophiodon elongatus* fish no. 9 (64.0 cm male) captured from site C, moved 2.8 km south to release site R, and monitored 19–27 April. S = stationary, L = temporarily lost.

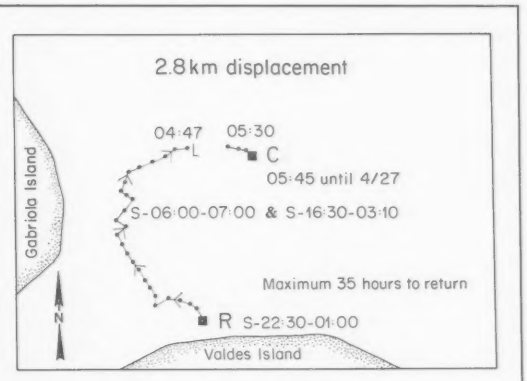


Figure 4
Positions of *Ophiodon elongatus* fish no. 10 (64.5 cm male) captured from site C, moved 2.8 km south to release site R, and monitored 23–27 April. S = stationary, L = temporarily lost (04:47–05:30).

signals became quite strong, suggesting homing lingcod were traversing areas without much rock relief. Lingcod encountered the deepest water (35 m) when crossing open areas. The four lingcod returned to their original capture sites where they remained until the transmitter batteries died or the tracking project was completed.

The first displaced fish (no. 7, a 66.2 cm male) was caught on 12 April in 10 m of water, moved 1 km south, and released in 18 m of water (Fig. 2). Because this was the first release and I did not know what movement to expect, I stayed directly over the fish from release time (16:40) until 20:30. However, no movement was detected. When I returned the following morning (07:30), the fish had moved about halfway (500 m, Fig. 2) back to the capture site. I stayed with the fish from 07:30 to 16:30, but no additional movement was detected. When tracking resumed the following morning (07:00), the fish was back at the original capture site where it remained for 12 d (until 25 April) when the battery apparently died. This fish moved at least 1 km, the displacement distance, in ~40 h. Because all homeward movement of the fish apparently occurred at night, the remaining displaced fish were tracked at night.

Fish no. 9 (64.0 cm male) was captured on 19 April in 12 m of water, tagged and moved 2.8 km south, and released into water 18 m deep (Fig. 3). It was stationary from release at 22:30 until 04:00 when it moved in a northerly direction for 2 h and stopped. Tracking was terminated at 07:15; when it reconvened at 18:30, the fish was in the same location. At 01:00 it moved to the northwest and the northeast until 04:30 when its signal was lost. Tracking was terminated at 08:30, and when it resumed at 17:15 the fish was back at the capture site. I assumed that the fish homed between 04:30 (when the signal was lost) and daybreak because all other lingcod movement occurred at night. It remained at the capture site for 7 days until tracking ended on 27 April. The 2.8 km return trip was completed in less than 60 h.

Fish no. 10 (64.5 cm male) was captured in 10 m of water, tagged and displaced 2.8 km south, and released in water 18 m deep (Fig. 4). The fish was stationary for 2.5 h after release (22:30–01:00) and moved sporadically from 01:00 to 06:00. The fish was stationary from 06:00 to 07:00 when tracking ended. When tracking

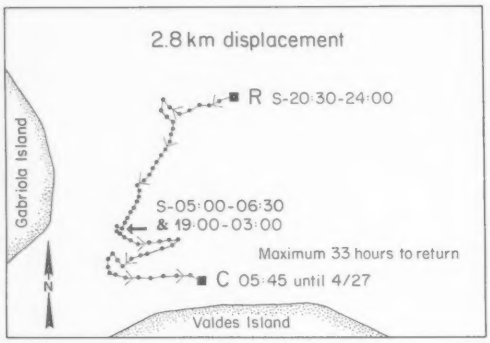


Figure 5
Positions of *Ophiodon elongatus* fish no. 11 (69.5 cm male) captured from site C, moved 2.8 km north to release site R, and monitored 25–27 April. S = stationary.

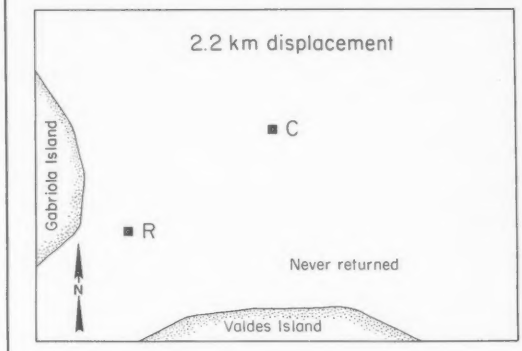


Figure 6
Positions of *Ophiodon elongatus* fish no. 8 (57.0 cm male) captured from site C, moved 2.2 km south to release site R, and monitored 16–27 April.

reconvened at 16:30, the fish was in the same position where it remained until 03:15. It then moved from 03:15 to 04:47 when the signal was temporarily lost. When relocated at 05:30, it was followed back to the capture site (05:30–05:45). It was at this site 4 days later that tracking stopped. The 2.8 km return trip took about 35 h.

Fish no. 11, a 69.5 cm male, was captured in 15 m of water, tagged and displaced 2.8 km to the north, and released in 12 m of water (Fig. 5). The fish remained stationary from release (20:30) until 24:00, when it moved to the west and south until 05:00. It remained at this position until tracking ended at 06:30. Later that day, the fish was relocated in the same location where it remained until 03:00. At this time the fish moved southeast and southwest and reached its original capture site at 05:45. It remained there until 27 April when tracking ended. The 2.8 km return trip took ~33 h.

One fish did not return from displacement. Fish no. 8, a 57.0 cm male was caught, tagged, and transplanted 2.2 km (Fig. 6) to the release site. Tracking continued for 12 d, during which time the fish apparently remained at the release site and no movement was detected. Because I was unable to make scuba observations at this site, it is possible that the tag was shed, which would also result in a stationary signal.

Lingcod took 33–60 h to return from their 1.0–2.8 km displacements for an average homing speed of 59.5 m/h (Table 1). Actually, their movement rate was faster since they moved only at night. If averaged over the total period when movement was documented (6 h, 24:00–06:00) for two consecutive nights (total of 12 h) then the rates are 83.3–233 m/h ($\bar{x}$ 195.8 m/h or 1175.0 m/d).

Discussion

Similar to intertidal fishes (Williams 1957) and several species of rockfishes (Carlson and Haight 1972, Matthews 1990), lingcod are another rocky reef fish capable of homing. Ultrasonic tracking is limited by low sample sizes due to tag cost and labor-intensive tracking. This study represents the first attempt to use ultrasonic telemetry to research lingcod movement behavior, but this was limited to displaced males soon after their nesting season. Additional work is necessary to determine whether males behave differently (e.g., do not home) at other times of the year. Telemetry would also be valuable to determine whether females make inshore-offshore movements to relocate previously used areas.

Lingcod movement occurred at night (24:00–06:00, Figs. 3–5) sometimes under dark, moonless skies. Little work has been done on fish vision in cold-temperate water systems (see review in Loew and McFarland 1990). Nevertheless, water at night is darker and has lower visibility than during the day, and as Ebeling and Bray (1976) point out, "...the relatively turbid, temperate waters are often a dark and gloomy place at night." Moreover, during our April tracking study, most nights were overcast and rainy, further reducing the water's visibility. The low visibility at night presumably precludes lingcod from using visual landmarks which usually requires precise recognition of specific features such as coral heads or rocks (Hasler 1966, Reese 1989). Still, an important question remains: Why should lingcod move at night when visibility is better during the day? Perhaps their nocturnal movement is to avoid predation since lingcod some-

times crossed flat, open areas that had no hiding places. Locally, harbor seals feed on lingcod, and recently their numbers have dramatically increased (Olesiuk et al. 1990). On the other hand, perhaps lingcod are simply more active at night, as my nighttime home-range observations indicated, which would explain their nighttime movement.

Lingcod homing was fairly directional and confined to the immediate area of Gabriola Island. In contrast, when displaced shorter distances (500 m), copper and quillback rockfishes, which co-occur with lingcod, moved along a bimodal northwest–southeast axis and sometimes retraced that path before finally moving in a westerly direction that led to their home site (Matthews 1990). After displacement, initial movement of lingcod was in the homeward direction only, i.e., no back-and-forth movement between the release site and home site was observed. The more direct and nocturnal homing in lingcod suggests they are navigating rather than orienting along one compass course or relying on olfactory cues. Orientation can be ruled out (Baker 1978, Able 1980) because lingcod successfully homed from north and south displacements. It is currently unknown whether rocky-reef fish, including lingcod, recognize olfactory cues.

Lingcod homing was fast in comparison with copper and quillback rockfishes, which took 8–25 d to return from 500 m displacements (Matthews 1990). From an analysis of a large-scale tagging program during 1982–87, Smith et al. (1990) estimated that mean dispersal rates for male and female lingcod were 500 m/d and 1040 m/d, respectively, similar to those observed in the present study (1173.7 m/24 h). Presumably, lingcod movement rates vary depending upon seasonal requirements (e.g., feeding, spawning, etc.).

Several hypotheses could explain why the smallest male (no. 8) did not return from displacement. Perhaps lingcod do not develop a resident or homing response until they are older and larger. The length-maturity relationship is determined by their geographic area (Richards et al. 1990), and the 50% maturity level for male lingcod at a similar latitude off the west coast of Vancouver Island is 57.1 cm. Thus, if fish no. 8 (57.0 cm) was not sexually mature, it may have lacked the ability to home. Buckley et al. (1984) also noted a lack of homing in small male lingcod. In that study, after 4.5 yr, the smallest transplanted lingcod (a 57 cm male) remained close to the release site after most transplanted lingcod had apparently homed. Alternatively, the lack of homeward movement could be due to tag shedding, which would also produce a stationary signal.

This study revealed new information on lingcod homing behavior. After displacement up to 2.8 km, lingcod moved at night back to home sites within 60 h and followed a fairly direct route. Because this was a pilot study and I displaced only male lingcod, more tracking studies are needed to increase sample sizes, include females, and attempt longer-distance transplants. Whether they home and reuse spawning areas will be important to document, as this information is crucial if lingcod preserves are established. It does appear that transplant attempts to rebuild lingcod stocks may be ineffective with larger, older males but may be successful if the lingcod are moved before they reach a certain size or age.

Acknowledgments

Claudia Hand, John Candy, and Bronwyn Lewis ably caught the lingcod and assisted in all phases of the field work including the tortuous all-night trips. This research was conducted while I held a Natural Sciences and Engineering Research Council Visiting Scientist Fellowship at the Canadian Department of Fisheries and Oceans Pacific Biological Station under the sponsorship of Dr. Laura Richards. The Institute of Ocean Sciences in Sidney kindly loaned us the use of the research vessel *Orca*. Dr. Richards and two anonymous reviewers provided helpful comments which greatly improved the manuscript.

Citations

Able, K.P.
1980 Mechanisms of orientation, navigation, and homing. *In* Gauthreaux, S.A. Jr. (ed.), Animal migration, orientation, and navigation, p. 283–373. Academic Press, NY.

Baker, R.R.
1978 Evolutionary ecology of animal migration. Holmes and Meier Publ., Inc., NY, 1012 p.

Buckley, R., G. Hueckel, B. Benson, S. Quinnel, and M. Canfield
1984 Enhancement research on lingcod (*Ophiodon elongatus*) in Puget Sound. Wash. Dep. Fish. Prog. Rep. 216, 93 p.

Canadian Hydrographic Service
1990 Canadian tide and current tables. Pacific Coast, vol. 5.

Carlson, H.R., and R.E. Haight
1972 Evidence for a home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish. Res. Board Can. 29: 1011–1014.

Cass, A.J., R.J. Beamish, and G.A. McFarlane
1990 Lingcod (*Ophiodon elongatus*). Can. Spec. Publ. Fish. Aquat. Sci. 109, 40 p.

Ebeling, A.W., and R.N. Bray
1976 Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. Fish. Bull., U.S. 74:703–717.

Gerking, S.D.
1959 The restricted movement of fish populations. Biol. Rev. Camb. Philos. Soc. 34:221–242.

Hart, J.L.
1943 Migration of lingcod. Fish. Res. Board Can., Prog. Rep. Pac. Coast Stn. 57:3–7.

Hasler, A.D.
1966 Underwater guideposts. Univ. Wisc. Press, Madison, 155 p.

Holland, K., R. Brill, S. Ferguson, R. Chang, and R. Yost
1985 A small vessel technique for tracking pelagic fish. Mar. Fish. Rev. 47(4):26–32.

Jagielo, T.H.
1990 Movement of tagged lingcod *Ophiodon elongatus* at Neah Bay, Washington. Fish. Bull., U.S. 88:815–820.

Loew, E.R., and W.N. McFarland
1990 The underwater visual environment. *In* Douglas, R., and M. Djamgoz (eds.), The visual system of fish, p. 1–43. Chapman and Hall, London.

Mathews, S.B., and M. LaRiviere
1987 Movement of tagged lingcod, *Ophiodon elongatus*, in the Pacific Northwest. Fish. Bull., U.S. 85:153–159.

Matthews, K.R.
1990 An experimental study of movement patterns and habitat preferences of copper, quillback, and brown rockfishes on three habitat types. Environ. Biol. Fishes 29:161–178.

Matthews, K.R., T.P. Quinn, and B.S. Miller
1990 Use of ultrasonic transmitters to track demersal rockfish movements on shallow rocky reefs. *In* Parker, N.C., et al. (eds.), Fish marking techniques, p. 375–379. Am. Fish. Soc. Symp. 7, Bethesda.

Miller, D.J., and J.J. Geibel
1973 Summary of blue rockfish and lingcod life history histories; a reef ecology study; and giant kelp *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish. Bull. 158:1–137.

Olesiuk, P.F., M.A. Bigg, G.M. Ellis, S.J. Crockford, and R.J. Wigen
1990 An assessment of the feeding habits of harbour seal (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. 1730, 135 p.

Reese, E.S.
1989 Orientation behavior of butterflyfishes (family Chaetodontidae) on coral reefs: Spatial learning of route specific landmarks and cognitive maps. Environ. Biol. Fishes 25:79–86.

Richards, L.J., and C.M. Hand
1991 Lingcod. *In* Fargo, J., and B.M. Leaman (eds.), Groundfish stock assessments for the west coast of Canada in 1990 and recommended yield options for 1991, p. 19–42. Can. Tech. Rep. Fish. Aquat. Sci. 1778.

Richards, L.J., J.T. Schnute, and C.M. Hand
1990 A multivariate maturity model with comparative analysis of three lingcod (*Ophiodon elongatus*) stocks. Can. J. Fish. Aquat. Sci. 47:948–959.

Smith, B.D., G.A. McFarlane, and A.J. Cass
1990 Movements and mortality of tagged male and female lingcod in the Strait of Georgia, British Columbia. Trans. Am. Fish. Soc. 119:813–824.

Williams, G.
1957 Homing behavior of California rocky shore fishes. Univ. Calif. Publ. Zool. 59:249–284.

An investigation of bottlenose dolphin *Tursiops truncatus* deaths in East Matagorda Bay, Texas, January 1990

W. George Miller
Naval Ocean Systems Center, Code 514, San Diego, California 92152

There are reports of massive mortalities of bottlenose dolphins *Tursiops truncatus* over periods of months in areas as large as the U.S. Atlantic coast and the Persian Gulf. From early June 1987 until March 1988, over 740 bottlenose dolphins (estimated at about 50% of the coastal migratory stock) stranded along the U.S. Atlantic coast from New Jersey to Florida (Scott et al. 1988, Geraci 1989). Geraci concluded the dolphins were poisoned by brevetoxin, a neurotoxin produced by the red tide organism *Ptychodiscus brevis*.

During 23 August to 30 October 1986, 527 dead dolphins were found on the eastern and western shores of the Persian Gulf. Several dead turtles, dugongs, and one 6.1 m unidentified whale were also found, along with many fish that washed ashore. Of the 78% of mammal carcasses identified to species, 64% were bottlenose dolphins, 34% were humpback dolphins *Sousa chinensis*, 1.7% were common dolphins *Delphinus delphis*, and 0.3% were finless porpoises *Neophocoena phocoenoides*. The dead dolphins included adults, neonates, calves, and juveniles. Cause(s) of the deaths could not be determined, since only four animals were necropsied (Anonymous 1986).

The subject of this study is an unusual stranding of 26 *T. truncatus* that occurred in January 1990 around East Matagorda Bay (EMB), Texas. There are no previous reports of this number of strandings in a relatively small area in a single day. On 20 January 1989, a helicopter pilot reported the stranded dolphins to the U.S. Coast Guard, who notified the Texas Marine Mammal Stranding Network at Texas A&M University and Texas Parks & Wildlife Department (TPW). These organizations collected 26 carcasses, 23 from within the Bay and 3 from the Gulf side of East Matagorda Peninsula. I performed necropsies on the dolphins on 24–25 January to determine cause of death.

Methods

Examination of dolphins

Each *T. truncatus* dolphin was assigned an identification number and its stranding location noted (Fig. 1). State of decomposition was noted: freshly dead with no bloating (1 animal), detectable bloating, or severe decomposition. Animals were sexed and weighed, and length was measured via a straight-line from the notch in the tail flukes to the most rostral aspect of the mandible. Measurements of blubber thickness were taken at six locations along the animal's left side using the standard protocol of the Naval Ocean Systems Center (NOSC) (Fig. 2). Skin condition and abnormal marks or deteriorated areas were recorded. Condition and position of thoracic and abdominal organs were noted before removal and collection of tissue samples.

Site inspection and background information

On 26 January 1990, I conducted an aerial survey of the stranding site, comparing the actual configuration of East Matagorda Bay with an existing map (NOAA nautical chart #11319) to determine exit routes for dolphins from the Bay to the deeper waters of the outer coast. The main exit is a narrow cut connecting the Bay and the Gulf (Fig. 1).

The Texas Parks and Wildlife Department monitored water-temperature changes in the Bay almost daily during 15–29 December 1989 (Fig. 3). The Bay was completely frozen over for 2.5 days with partial ice remaining for 4 days. On 22 December, a helicopter pilot flew close to the Bay to observe about 12 dolphins swimming and breaking ice (~5 cm thick) in a 4–7 km area in the east-central region of the Bay.

Rapidly-moving weather systems from the north with strong northerly winds can significantly lower tidal levels in the Bay (Steve Marwitz, Texas Parks & Wildlife, Rockport, TX 78382, pers. commun.). Within the period 15–22 December 1989, when two cold-weather systems moved through the area, an estimated range for the mean low tide level was 30–60 cm below normal (Mark Mazot, Tex. Parks Wildl. Dep., pers. commun., Feb. 1990); however, there were no official measurements. Thus it is possible that lowered water depths around the periphery of the Bay could have impeded dolphin movement between the Bay and the Gulf of Mexico via the Caney Creek Gulf Cut or the intercoastal canal.

Results

Of the 26 *Tursiops truncatus* examined, 23 dolphins were from within East Matagorda Bay and consisted of 6 mature males (MM), 5 immature males (IM), 7 mature

Manuscript accepted 9 September 1992.
Fishery Bulletin, U.S. 90:791–797 (1992).

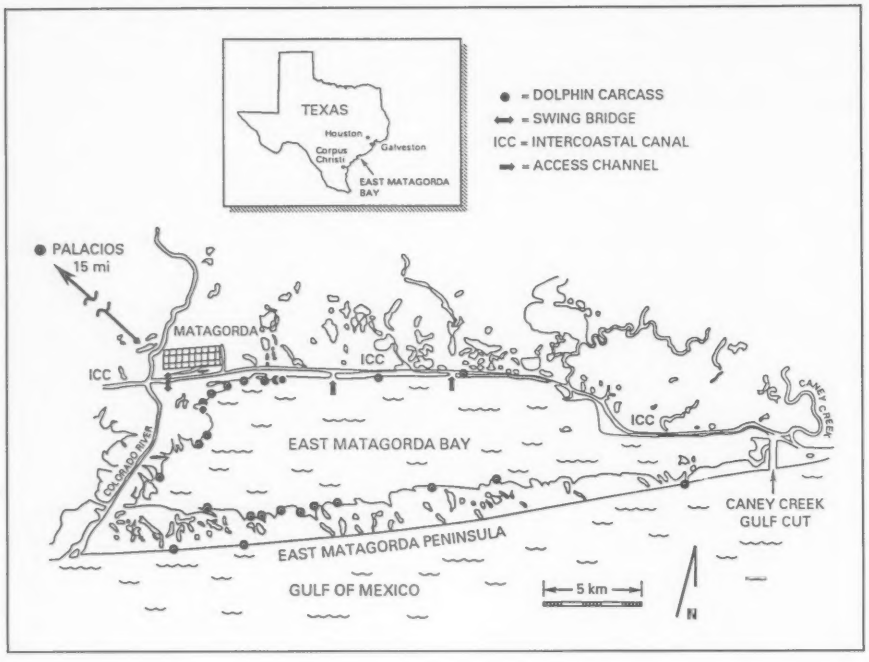
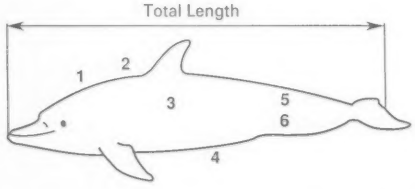


Figure 1
Map of East Matagorda Bay, Texas, showing location of recovered bottlenose dolphin carcasses.



Site 1) Dorsal midline 10cm to 15cm caudal to the blow hole.
Site 2) Dorsal midline 10cm to 15 cm cranial to the insertion of the dorsal fin.
Site 3) Lateral midline at the midpoint of the dorsal fin.
Site 4) Ventral midline 10cm cranial to umbilicus.
Site 5) Dorsolateral aspect of tail stock at level of the anus.
Site 6) Lateral midline at level of the anus.

Figure 2
Blubber measurement sites on bottlenose dolphins collected in East Matagorda Bay, based on Naval Ocean System Center collection procedures.

females (MF) (4 with fetus), and 5 immature females (IF); 2 females and 1 male were from outside the Bay on East Matagorda Peninsula. I could not make an accurate determination of time of death because decomposition varies markedly depending on environmental conditions. The condition of the carcasses at necropsy suggested that death occurred ~5–10 days prior to siting, with the exception of one freshly dead animal collected outside the Bay on East Matagorda Peninsula.

Table 1 shows blubber thickness measured at NOSC (site 2), length, sex, and weight data from 24 East Matagorda Bay dolphins for which there were complete data, and from a comparison group of 16 Texas coast dolphins which stranded over the period 1981–89. Average blubber thickness for 21 stranded dolphins recovered in the Bay was 12.7 mm, while the average thickness for the comparison group of 16 dolphins recovered on the Texas coast during the winter months of November–March 1981–89 was 18.6 mm at the same measurement site. This difference was significant (Student's t test, $P<0.001$). In addition, the subcutaneous fat layer that is prominent between the blubber and skeletal muscles in healthy robust dolphins (Ridgway and Fenner 1982) was greatly reduced or absent in all of the dolphins taken from inside the Bay.

A linear regression was used to (1) show the relationship of blubber thickness (mm) to weight (kg) for the comparison group of dolphins stranded along the Texas coast during winter months and (2) test the similarity of slopes between the Texas-coast and East Matagorda Bay groups (Fig. 4). In Texas coast strandings, there was a significant positive correlation between blubber thickness and body weight (r 0.9); while in the Bay group, blubber thickness decreased with increased weight (r −0.38).

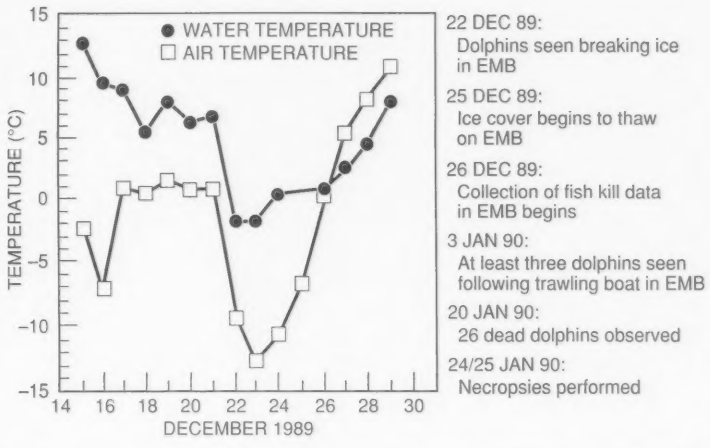


Figure 3

Water and air temperatures at East Matagorda Bay (EMB) during December 1989, and chronology of significant events related to January 1990 strandings of bottlenose dolphins. Air temperatures recorded at Palacios, Texas (the closest recording weather station, 15 mi away), (from Naval Oceanogr. Command Detachment, Asheville, NC). Water-temperature data from Texas Parks & Wildl. Dep., Fish. Div., Coastal Branch, Palacios, TX. Water temperatures in East Matagorda Bay for the dates 1, 15, and 29 January 1992 were 13.5, 16, and 14.5°C, respectively.

Two mature females (MF) and a mature male (MM) had thickened hepatic capsules. One MF had marked lobulation and increased fibrous tissue throughout the liver. Five mature animals (2 MM, 3 MF) had an unusual and unidentified thin, smooth creamy-white layer on the endothelial surface of the hepatic portal vessels.

Three animals had abnormalities associated with the gastrointestinal (GI) system. An immature female (IF) had a section of small

Table 1

Summary data from 24 bottlenose dolphins *Tursiops truncatus* taken in East Matagorda Bay and Peninsula, January 1990, and from Texas coast bottlenose dolphins recovered in November–March 1981–89 (data from Texas Marine Mammal Stranding Network).

East Matagorda				Texas coast			
Blubber thickness (mm)	Length (cm)	Sex	Weight (kg)	Blubber thickness (mm)	Length (cm)	Sex	Weight (kg)
Peninsula				12	100	F	14
9	198	M	68	12	115	M	17
15	240	F	123	15	205	F	91
28	235	F	NA	16	212	M	104
Bay				17	219	M	109
4	216	M	114	18	177	F	59
5	269	M	182	18	206	F	107
5	282	F	170	18	221	F	102
7	262	F	139	18	235	F	139
8	288	M	189	18	240	F	141
9	262	M	159	18	235	F	143
10	275	M	180	20	227	M	136
11	176	F	43	20	179	M	120
11	216	F	91	24	280	M	150
11	270	M	170	25	237	M	193
13	191	M	55	28	260	M	216
13	258	M	141				
14	207	F	82				
15	245	F	114				
15	261	F	136				
15	255	F	150				
15	256	F	166				
16	256	M	150				
22	220	F	82				
22	254	F	145				
26	218	M	77				

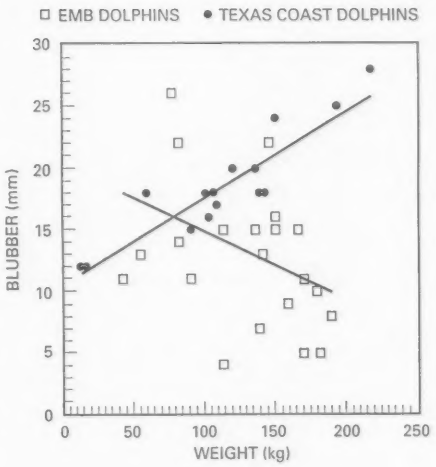


Figure 4

Linear regression of blubber thickness and weight for bottlenose dolphins recovered from East Matagorda Bay, in January 1990, and for comparison group of bottlenose dolphins from the Texas coast during November–March 1981–89.

intestine ~1.5 m long containing extremely-hard dehydrated feces, and its stomach contained partially-digested fish and bones. Two IF had peritoneal adhesions throughout the GI tract. One of these had a serofibrinous exudate on the serosal surfaces of the entire small intestine, and the gastric compartments were empty. Four animals (2 MF, 2 IM) had nematodes in the forestomach and fundic chamber. Clear, crystallized deposits adhered to the parietal and visceral surfaces of the thoracic and abdominal cavities of all animals. These deposits were ≤1 mm in size, felt "gritty," and imparted a "sandpaper-like" texture to the surface, a condition not uncommon in decomposed dolphins in the region (Raymond J. Tarpley, Texas A&M Univ., College Station, pers. commun., March 1990).

Every mature animal in the Bay group had hard, white, spherical deposits in the pancreatic interstitial tissue. These deposits were ≤2 mm in size and were scattered throughout the central pancreas. When crushed with a knife, the deposits were the same white color and consistency throughout.

Stomach contents were noted in 19 of the 23 Bay animals. Stomachs of 6 animals (3 MM, 2 IF, 1 MF) were void of food. Ten animals had unidentified fish, bones, and scales in the stomach. Three animals (2 MF, 1 IM) had undigested and partially-digested fish in the forestomach; in two of these animals, there was a 30 cm undigested fish in the esophagus.

No other gross abnormalities were noted in the respiratory, cardiovascular, renal, musculoskeletal, or reproductive systems of the Bay dolphins. Eyes were too decomposed for examination. Data concerning infectious agents (viral, bacteriological, fungal, etc.) could not be obtained because of advanced decomposition of the carcasses.

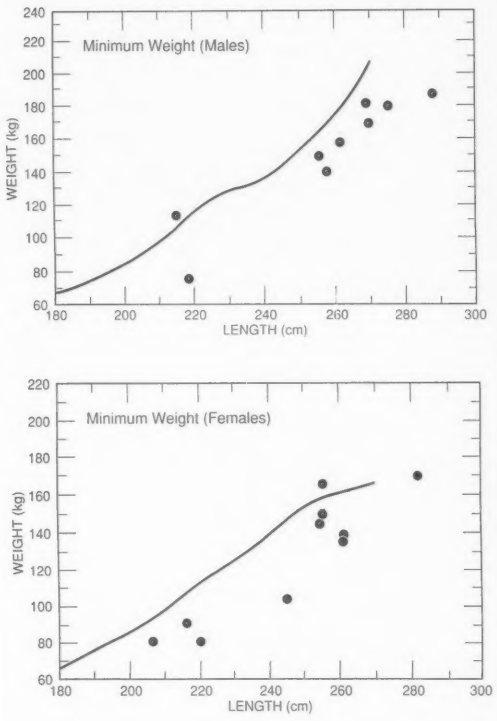


Figure 5
Weight-length data for male and female bottlenose dolphins from East Matagorda Bay, plotted on Ridgway and Fenner's (1982) minimum weight-length graph.

Discussion

Several factors might have contributed to the East Matagorda Bay dolphin mortality. First, an abnormally rapid drop in water temperature which resulted in the Bay freezing over; second, abnormally low tidal levels, possibly preventing exit from the Bay; and third, striped mullet, an important food source for the dolphins, may have been significantly depleted by the freeze. The poor condition of Bay dolphins was indicated by the ~89% of males and 80% of females in states of emaciation or near-emaciation, based on minimum weight-length guidelines established by Ridgway and Fenner (1982) (Fig. 5). In addition, average blubber thickness of the Bay dolphins was a third less than that of the Texas-coast dolphins during winter, based on records over the previous 9-year period.

Gunter (1941) and Gunter and Hildebrand (1951) reported on the death of fishes and other organisms during severe cold periods along the Texas coast. In 1940, water temperature fell from 18.3°C to −3.9°C in 4 hours (Gunter and Hildebrand 1951). Concerning dolphins, Gunter (1941) write, "It is probably worth recording that two porpoises, T. truncatus, were stranded in St. Charles Bay by the low tide and were forced to remain there, only partially submerged, during the coldest days of the freeze. They did not die and it was reported that they escaped when the tide rose." There are other reports of bottlenose dolphins in frozen seas; for example, Manton (1986) reports that *T. truncatus* have been seen breaking ice in the northern part of the Adriatic Sea. There are no records of dolphin deaths associated with other recent freezes in East Matagorda Bay, i.e., in 1983–84 or February 1989; however, local fishermen stated that the only previous sightings of dead dolphins (reported as 4 or 5) in the Bay followed the 1983–84 storm. No data on water

temperatures or duration of ice on the Bay was available for the 1983–84 freeze.

There may have been no possible escape route for the dolphins because of the very low water level and the ice formation on the surface of the Bay. Smith et al. (1983) state that ice may impede the movement of dolphins in an area, and Shane (1980) studied the distribution of bottlenose dolphins in southern Texas and found that some animals had a home range that was limited to shallow bays. In our study, local fishermen stated that they repeatedly saw the same animals, which they could recognize by marks on the dorsal fin and flukes, and that the approximate number of dolphins in the Bay usually was "in the 20's." If the dolphins in East Matagorda Bay were resident, then many of the older animals stranded in January 1990 likely had experienced and survived the severe weather conditions in 1983 when the Bay froze over.

There are no precise data available to accurately determine the food biomass available to the EMB dolphins during and after the December 1989 freeze, but it is possible that an essential food source was not available. Fish mortality is greatest during a rapid decrease in water temperature (Springer and Woodburn 1960). Data from Dailey et al. (1991a) show that the relative abundance (gillnet entrapment technique, n/hour) of subadult and adult striped mullet *Mugil cephalus* along the Texas coast in spring 1989 was double that of previous years, while the relative abundance (bag-seine entrapment technique, n/ha) of juveniles in 1989 was only 60% of the value for the two previous years. Following the December 1989 freeze, the relative abundance of subadult and adult striped mullet in the spring of 1990 was far below that of spring 1989, while the relative abundance of juveniles (for recruitment to the population) was 380% higher in 1990 than it was in 1989. The large increase in relative abundance of young for spring recruitment to the population following the December 1989 freeze has been attributed to a lack of adult predator fish (Lawrence McEachron, Texas Parks Wildl., Rockport, TX 78382, pers. commun., Oct. 1991).

Table 2 shows estimated freeze kills for a variety of marine fish species in East Matagorda Bay for periods in 1983–84, February 1989, and December 1989 (McEachron et al. 1991). Although freezes are common on the Texas coast, fish kills of the magnitude of the December 1989 freeze in the Bay had never before been recorded, with *Mugil cephalus* mortality estimated to be over 2.5 million fish.

And thus, a compounding problem for the dolphins in the December 1989 freeze is the unprecedented kill of striped mullet. It is probable that a food source essential to the Bay dolphins was severely depleted at a critical time when the dolphins needed calories. Barros (1992), Barros and Odell (1990), and Cockcroft and Ross (1990) show that bottlenose dolphins utilize a variety of food resources, composed primarily of fish (4 to 6 major prey species common to their respective areas) and cephalopods (primarily 1 species common to their respective areas), and occasionally crustaceans. Pryor et al. (1990) suggest that mullet has been a staple dolphin food for centuries. Gunter (1942) reported on prey in freshly-killed, presumably-healthy *T. truncatus*: 1 from deeper waters and 33 from the shallows of Aransas and St. Charles Bays, Aransas County, Texas.

Table 2

Estimated marine fish-freeze kill in East Matagorda Bay for the periods 1983–84, February 1989, and December 1989 (McEachron et al. 1991). ND = no data.

Species	1983–84	February 1989	December 1989
Micropogonias undulatus			
Atlantic croaker	700	100	<100
Pogonias cromis			
Black drum	3300	89,900	5600
Brevoortia patronus			
Gulf menhaden	7100	100	2400
Arius felis			
Hardhead catfish	ND	200	ND
Lagodon rhomboides			
Pinfish	300	200	100
Sciaenops ocellatus			
Red drum	500	23,500	400
Cynoscion arenarius			
Sand seatrout	ND	ND	ND
Archosargus probatocephalus			
Sheepshead	4300	11,600	200
Leiostomus xanthurus			
Spot	ND	ND	ND
Paralichthys lethostigma			
Southern flounder	ND	ND	ND
Cynoscion nebulosus			
Spotted seatrout	900	170,400	600
Mugil cephalus			
Striped mullet	**178,400**	**21,200**	**2,684,100**
Other fish	19,400	67,400	6,400
Total fish	214,900	384,600	2,699,800

Although Gunter found 12 species of fish and 1 shrimp, 83% of fish consumed were *Mugil cephalus*.

A significant difference between stranded (presumably ill) and net-caught/capture-killed (presumably healthy) dolphins is that stranded dolphins (Barros 1992, Barros and Odell 1990) have a high percentage of empty stomachs (empty or <1 g, 32–54%) while net-caught or captured dolphins (Cockcroft and Ross 1990, Gunter 1942) have a very low percentage of empty stomachs (<3%). The reason for this discrepancy is not documented, but ill dolphins often have a decreased appetite or may not be able to catch food. Another reason for a high percentage of empty stomachs in the Bay dolphins may be lack of food availability. Of 19 Bay dolphins examined, 32% had empty stomachs and 37% had only unidentifiable bones and scales (no flesh). Gunter (1942) observed 34 killed specimens of *T. truncatus*; none of the stomachs were void of food. In addition, Gunter (1942) showed that the average number of recognizable fish/stomach was 18, whereas the 15% of EMB dolphins that had eaten recently had no more than 2 recognizable fish/stomach. These data, along with the Texas Parks & Wildlife fish freeze-kill and biomass data, indicate that food was in short supply for the Bay dolphins. I suspect that many of them might have survived if they had sufficient nutrition.

Ridgway and Fenner (1982) state that the blubber may thin as weight loss progresses to emaciation, and reduced blubber thickness at necropsy is one sign of emaciation. Studies on healthy, well-fed dolphins at the Naval Ocean Systems Center in San Diego show that *T. truncatus* have thicker blubber as body weight increases, and that *T. truncatus* may respond within 2 weeks to water-temperature changes by increasing or decreasing blubber thickness for cooler or warmer temperatures, respectively (William A. Friedl, NOSC, Kaneohe, HI, pers. commun., Nov. 1990). Level of starvation may not be the only reason for differences in blubber thickness between EMB and Texas coast dolphins: the EMB dolphins might originally have had thinner-than-normal blubber resulting from living in a shallow bay with higher-than-average water temperatures (29, 25, and 19°C monthly average water temperatures in EMB for September, October, and November 1989, respectively); or the normal prey field in EMB might be limited compared with other areas. Further work on blubber constituents and factors affecting blubber thickness is needed to determine if blubber thickness is an indicator of starvation as a cause of death.

The December 1989 EMB freeze, in which temperatures stayed near freezing for about 4 days, resulted in devastation of the dolphins' most-likely major food source, the striped mullet. The dolphins' emaciated condition, the substantial reduction in their blubber thickness, lack of food in their stomachs, the assessment that dolphins lived for 2 weeks following the freeze, and the EMB fish freeze-kill and biomass data suggest, in addition to any direct effects to the dolphins of the extreme cold, that decimation of the food resource contributed to this acute dolphin mortality event.

Acknowledgments

I thank the following organizations and individuals for their contributions that made this report possible: Texas Marine Mammal Stranding Network (Dr. Raymond Tarpley, founder of the TMMSN; Gina Barron, for her untiring efforts and organizational skills; Elsa Haubold and all the other members of the network who have graciously devoted their time); Texas Parks and Wildlife Department (Steve Marwitz and Lawrence McEachron, Rockport, Texas); U.S. Coast Guard; Houston Helicopter (Mike Boyaki and Dave Beard); Dr. James Calvin, Department of Statistics, Texas A&M University, College Station; and Naval Oceanographic Command Detachment, Asheville, North Carolina. Special thanks to Dr. Sam H. Ridgway (Naval Ocean Systems Center) for his critique and support for this work, and to F.G. Wood for his suggestions. Dr. Raymond J. Tarpley (TMMSN and Texas A&M University), provided NOSC with information on blubber measurements taken from dolphins stranded on the Texas coast from 1981 to June 1989.

Citations

Anonymous
1986 Regional organization for the protection of the marine environment, Report of the first meeting of experts on mortality of marine animals, Kuwait, Nov. 22–23, 1986.

Barros, N.B.
1992 Food habits. *In* Hansen, L.J. (coordinator), Report on investigation of 1990 Gulf of Mexico bottlenose dolphin strandings, p. 41–46. Contrib. MIA-9293, NMFS Southeast Fish. Sci. Cent., Miami.

Barros, N.B., and D.K. Odell
1990 Food habits of bottlenose dolphins in the southeastern United States. *In* Leatherwood, S., and R.R. Reeves (eds.), The bottlenose dolphin, p. 309–328. Academic Press, San Diego.

Cockcroft, V.B., and G.J.B. Ross
1990 Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. *In* Leatherwood, S., and R.R. Reeves (eds.), The bottlenose dolphin, p. 295–308. Academic Press, San Diego.

Dailey, J.A., J.C. Kana, and L.W. McEachron
1991 Trends in relative abundance in size of selected finfish and shellfish along the Texas coast: November 1975–December 1989. Manage. Data Ser. 53, Texas Parks Wildl. Dep., Fish. Wildl. Div., Coastal Fish. Br., Austin, 241 p.

Geraci, J.R.
1989 Clinical investigation of the 1987–1988 mass mortality of bottlenose dolphins along the U.S. central and south Atlantic coast. Report to the National Marine Fisheries Service, U.S. Navy, Office of Naval Research, and the Marine Mammal Commission, April 1989.

Gunter, G.
1941 Death of fishes due to cold on the Texas coast, January, 1940. Ecology 22:203–208.
1942 Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montague), on the Texas coast, with particular reference to food habits. J. Mammal. 23: 267–276.

Gunter, G., and H.H. Hildebrand
1951 Destruction of fishes and other organisms on the south Texas coast by the cold wave of January 28–February 3, 1951. Ecology 32:731–736.

Manton, V.J.A.
1986 Water management. *In* Bryden, M.M., and R. Harrison (eds.), Research on dolphins, p. 189–208. Clarendon Press, Oxford.

McEachron, L.W., G.C. Matlock, C.E. Bryan, P. Unger, T.J. Cody, and J.H. Martin
1991 Winter mass mortality of animals in Texas bays. Texas Parks Wildl. Dep., Fish. Wildl. Div., Coastal Fish. Br., Austin, 47 p.

Pryor, K., J. Lindbergh, S. Lindbergh, and R. Milano
1990 A dolphin-human fishing cooperative in Brazil. Mar. Mammal Sci. 6(1):77–82.

Ridgway, S.H., and C.A. Fenner
1982 Weight-length relationships of wild-caught and captive Atlantic bottlenose dolphins. J. Am. Vet. Med. Assoc. 181(11):1310–1315.

Scott, G.P., D.M. Burn, and L.J. Hansen
1988 The dolphin die-off: Long-term effects and recovery of the population. Proc., Oceans '88, p. 819–823. IEEE, NY.

Shane, S.H.
1980 Occurrence, movements, and distribution of bottlenose dolphins, *T. truncatus*, in Southern Texas. Fish. Bull., U.S. 78:593–601.

Smith, T.G., J.R. Geraci, and D.J. St. Aubin
1983 Reaction of bottlenose dolphins, *Tursiops truncatus*, to a controlled oil spill. Can. J. Fish. Aquat. Sci. 40:1522–1525.

Springer, V.G., and K.D. Woodburn
1960 An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv. Prof. Pap. Ser. 1:1–104.

Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Morone saxatilis**

David H. Secor

The University of Maryland System, Center for Environmental and Estuarine Studies
Chesapeake Biological Laboratory, Solomons, Maryland 20688-0038

Management of Chesapeake Bay and coastal striped bass *Morone saxatilis* fisheries is affected by migration of large Chesapeake adults into coastal waters. Tagging studies during the 1930s and 1950s indicated that a small percentage of Chesapeake striped bass contribute to the coastal fishery (Vladykov and Wallace 1952, Mansueti 1961, Massman and Pacheco 1961). However, work on age- and sex-specific migration patterns (Chapoton and Sykes 1961, Kohlenstein 1981) suggested that about half of the females aged 3+ migrate out of the Bay. The current consensus appears to be that young striped bass remain in or near the tributary in which they were spawned for 2 or 3 years; thereafter most males remain in the Bay, while a substantial number of females migrate out of the Bay and remain in coastal waters until sexually mature (Chapman 1987, Setzler-Hamilton and Hall 1991). Although facultative anadromy is suggested by tagging studies, age- and sex-specific rates of anadromy remain largely unknown (ASMFC 1990).

Wave-length dispersive electron microprobe analysis of strontium/calcium ratio (Sr/Ca) in otoliths has recently been employed as a method for distinguishing between freshwater and marine life-history phases of individual fishes (Casselman 1982, Radtke et al. 1988, Kalish 1990). Sr is substituted for Ca into the lattice of aragonitic calcium carbonate (Kinsman and Holland 1969), and in otoliths the rate of substitution is in proportion to its abundance in the endolymph (Kalish 1989). Sr concentration in seawater is more than one order of magnitude greater than in freshwater (Bagenal et al. 1973, Radtke et al. 1988, Kalish 1990, Ingram and Sloan 1992). Therefore, Sr levels in otoliths of fish exposed to seawater should be substantially higher than those exposed to freshwater.

Sr/Ca ratio in otoliths of anadromous striped bass was analyzed to determine its usefulness in charting individual migratory histories. In a prospectus, Coutant (1990) suggested a similar application to investigate patterns of estuarine use by Chesapeake Bay and Roanoke River striped bass. Here, I looked for a seasonal pattern in otolith Sr/Ca ratios that was consistent with anadromous behavior. An annual cycle of low Sr/Ca ratios during spring (exposure to Sr-poor freshwater) and high ratios during fall and winter (exposure to Sr-rich saltwater) was expected in large adults. If such a pattern existed, then further research and application would be justified. Analysis of Sr/Ca composition could be applied to problems of migratory behavior, spawning, hatchery contribution to coastal stocks, definition of life-history traits, environmental degradation (Coutant 1990), and consequences of anadromy to recruitment (e.g., Kalish 1990).

In this investigation, I related Sr/Ca ratios to annuli which are assumed to form in spring (see Discussion). I used a less traditional definition for annulus, "...a ridge or a groove in or on the [hard] structure..." (Wilson et al. 1987), because opaque and translucent zones did not adequately describe the microstructure observed under scanning electron microscopy or light microscopy.

Methods

Sr/Ca ratios were examined for five large adults from the Chesapeake Bay and South Carolina (Table 1). Adults from the Chesapeake were presumed to be anadromous based on their size (Setzler-Hamilton and Hall 1991); the South Carolina population is a freshwater population, resident to the Santee-Cooper watershed (Secor et al. 1992). Chesapeake Bay fish (n 3) were collected by charterboat fisherman from Solomons, Maryland during the May 1991 "Maryland Trophy Season", presumably caught in upper Bay waters. South Carolina fish were collected at a 1989 fishing tournament. Otoliths were removed, cleaned in 10% sodium hypochlorite solution (bleach), and rinsed with deionized water. They were embedded in Spurr epoxy, sectioned in a transverse plane with a Buehler Isomet saw, and mounted on a glass slide. Otoliths were polished (see Secor et al. 1991) until all annuli were visible with transmitted light on a compound microscope. Otolith sections were further polished with 3μm alumina to limit any surface structure that could cause artifacts

* Contribution 2368, Center for Environmental and Estuarine Studies, The University of Maryland System.

Manuscript accepted 13 July 1992.
Fishery Bulletin, U.S. 90:798–806 (1992).

Table 1

Striped bass *Morone saxatilis* from Chesapeake Bay (MD and Juv) and Santee-Cooper (SC) populations used in electron microprobe analyses.

ID	Population	Sex	Age	TL (cm)	Weight (kg)
MD-1	Chesapeake	Female	21	119	15.5
MD-2	Chesapeake	?	8	94	7.3
MD-3	Chesapeake	?	9	93	8.1
SC-1	Santee-Cooper	Female	6	80	4.8
SC-2	Santee-Cooper	Female	5	81	5.4
Juv-1	Patuxent River	Juvenile	0	—	—

in microprobe analysis (Kalish 1991). Otolith sections were carbon-coated in a high-vacuum evaporator.

A sagitta from a juvenile striped bass sampled from the Patuxent River (Chesapeake Bay tributary) was similarly prepared and polished so that the core and all increments were sectioned (Secor et al. 1991). The juvenile's parentage, a 20 kg female that was assumed to be migratory based on its size (Kohlenstein 1981), was known because the juvenile was a marked hatchery fish released as a 9-day-old larva.

X-ray intensities for Sr and Ca elements were quantified using a JXA-840A JEOL wave-length dispersive electron microprobe (Central Facility for Microanalysis, Univ. Maryland, College Park MD 20742), with Calcite ($CaCO_3$) and Strontianite ($SrCO_3$) as standards. Striped bass otoliths were resilient to high-beam power densities compared with previous work on salmonid otoliths (Kalish 1990) and showed no diffusion of elements over a 32-sec counting period (Table 2). This permitted analysis of small sample points ($5 \times 5\,\mu m$) at high accelerating voltage (25 kV) and probe current (20 nA). Background and peak counting times were each 20 sec for Sr, and 5 sec for Ca. Background counting times were equally divided below and above the peak position. The detection limit for Sr was 580 ppm. Precision was calculated at <1% for Ca counts and 8.2% for Sr counts (at Sr/Ca = 0.003) (1.96σ; Goldstein et al. 1981). The electron beam caused a physical disruption (a pit) at the section's surface which limited the proximity of adjacent points that could be accurately sampled. Initial analyses of Chesapeake sample otoliths at "step" distances of $8\,\mu m$ resulted in no Sr X-ray counts. This was probably due to physical disruptions among adjacent points because surface structure can cause artifacts in microprobe analysis (Kalish 1991). Analysis was therefore conducted at 13 and $20\,\mu m$ step sizes where positive counts occurred (Table 3). Transects (700–$2600\,\mu m$ in length) across annuli in the otolith sections were selected. The electron microprobe sampled 60–130 points along these transects. Each point required ~70 sec of microprobe time. X-ray intensities were calculated using the ZAF procedure (Reed 1975), normalized to standards, and converted to elemental (atomic weight) ratios.

Due to their close proximity, individual points were not always visible in probed otolith sections. To relate Sr/Ca ratios to the

Table 2

Effect of counting time on strontium and calcium counts. Accelerating voltage = 25 kV, probe current = 20 nA, sample size = $5\,\mu m^2$. Note that Sr and Ca show no decline with counting time which would indicate sample destruction.

Seconds counted	Counts/sec	
	Sr	Ca
0	585	16763
4	586	16678
8	576	16725
12	589	16869
16	586	16748
20	578	16847
24	570	16828
28	592	16850
32	603	16813

Table 3

Summary statistics for Sr/Ca ratios of Chesapeake Bay and Santee-Cooper samples. All ratio statistics have been multiplied by 1000 for presentation purposes. Age is given in parentheses below each sample. Step = distance between sampled points along transect.

Sample	Transect	Step (μm)	N	$\bar{x}$	SE	Mode	Median
MD-1 (21)	1	20	99	2.753	0.094	3.4	2.8
	2	20	99	2.645	0.095	2.3	2.6
	3 (age ≥7)	13	60	3.713	0.124	4.7	4.0
MD-2 (8)	—	13	99	2.974	0.155	0	3.0
MD-3 (9)	1	20	100	2.385	0.097	2.8	2.4
	2	13	70	2.323	0.086	1.7	2.3
SC-1 (6)	—	20	130	0.937	0.061	0	0.9
SC-2 (5)	—	13	99	0.241	0.054	0	0

opaque zones of annuli checks, probed sections were viewed under a compound microscope and transect distances between annuli measured with an ocular scale. Because the distance between each microprobe measurement was known, distances between measurements can be converted to distances between annuli. Distances between annuli (annular increments) became narrow with increasing age (<50 μm) (Fig. 1), and points did not always sample directly on annuli. Therefore, it was necessary to assign an annulus to the closest sampled point. Points between annuli were assumed to sample age in linear proportion. For instance, if 10 points were sampled between annuli 5 and 6, then points would be assigned ages 5.0, 5.1, 5.2,...6.0. A replicate scan was performed on two of the otolith samples. In the juvenile's otolith, not all daily increments were visible along the transect with scanning electron microscopy or light microscopy. Therefore, Sr/Ca ratios were related to standard length using an otolith/fish-length relation documented for the Potomac River population (Houde and Rutherford 1992).

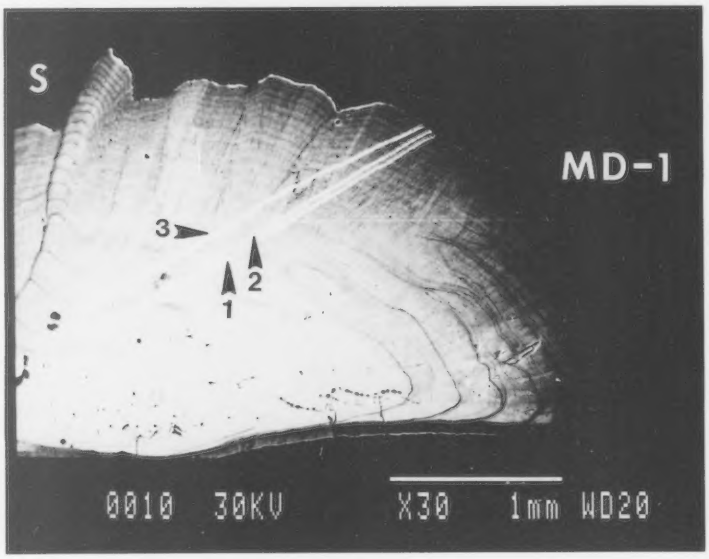


Figure 1
Back-scatter electron micrograph of otolith from striped bass *Morone saxatilis* Sample MD-1. Twenty-one annuli are clearly visible along the sulcus (s) and sulcal ridge. Transects 1 and 2 were performed at 20 μm step size; Transect 3 began at the 7th annular check and 13 μm step size. The probed transect previous to Transect 3 was performed at 8 μm step size and resulted in no positive Sr counts. Note that individual probed points are visible in a series of physical disruptions (pits) for Transects 1 and 2.

Results

Mean Sr/Ca ratios in Chesapeake striped bass were three to four times greater than Santee-Cooper striped bass (Table 3; Figs. 2,3). This trend is consistent with a salinity influence on the ratio, because Santee-Cooper striped bass are confined to freshwater and both Santee-Cooper females were sexually mature. Although substantial variation occurred in Sr/Ca between South Carolina samples, both samples were near the electron microprobe's detection limit of Sr/Ca (Sr/Ca =0.0008). Instrumental precision decreases markedly as the detection limit is approached, which may produce spurious variation. Peaks and nadirs in the Sr/Ca ratios were apparent in Chesapeake striped bass, and in fish >age-4, these patterns generally showed an annual cycle (Fig. 2). This is most apparent for sample MD-1. Because low Sr/Ca ratios can be associated with freshwater excursions, results indicate yearly migration for this large female.

Lack of agreement among replicate transects (Fig. 2) probably was due to the manner in which ages were assigned, spatial resolution, and within-sample variability. Probed points of replicate transects could not be directly "lined up" with respect to annuli. This offset occasionally resulted in the interpretation that an annuli was associated with a peak in one transect and a nadir in the other transect (e.g., annuli 15, 18, and 19 in Transect 1 vs. these annuli in Transect 2 for MD-1; Fig. 2). Transects 1 and 2 for Sample MD-1 (20 μm step size) sampled few points between successive annuli at older ages, and the accuracy with which points could be assigned to annuli was less (Fig. 4). Transect 3 for MD-1 (13 μm step size) clearly shows increased resolution of the ratio across annular increments. Similarly, Transect 2 (13 μm) for MD-3 revealed several more peaks and nadirs after the 5th annulus than did Transect 1 (20 μm). The overall Sr/Ca ratio was significantly different between Transects 1 and 2 for MD-3 (Table 4, t 3.06, $p<$ 0.01). Replicate transects in MD-1, where step size

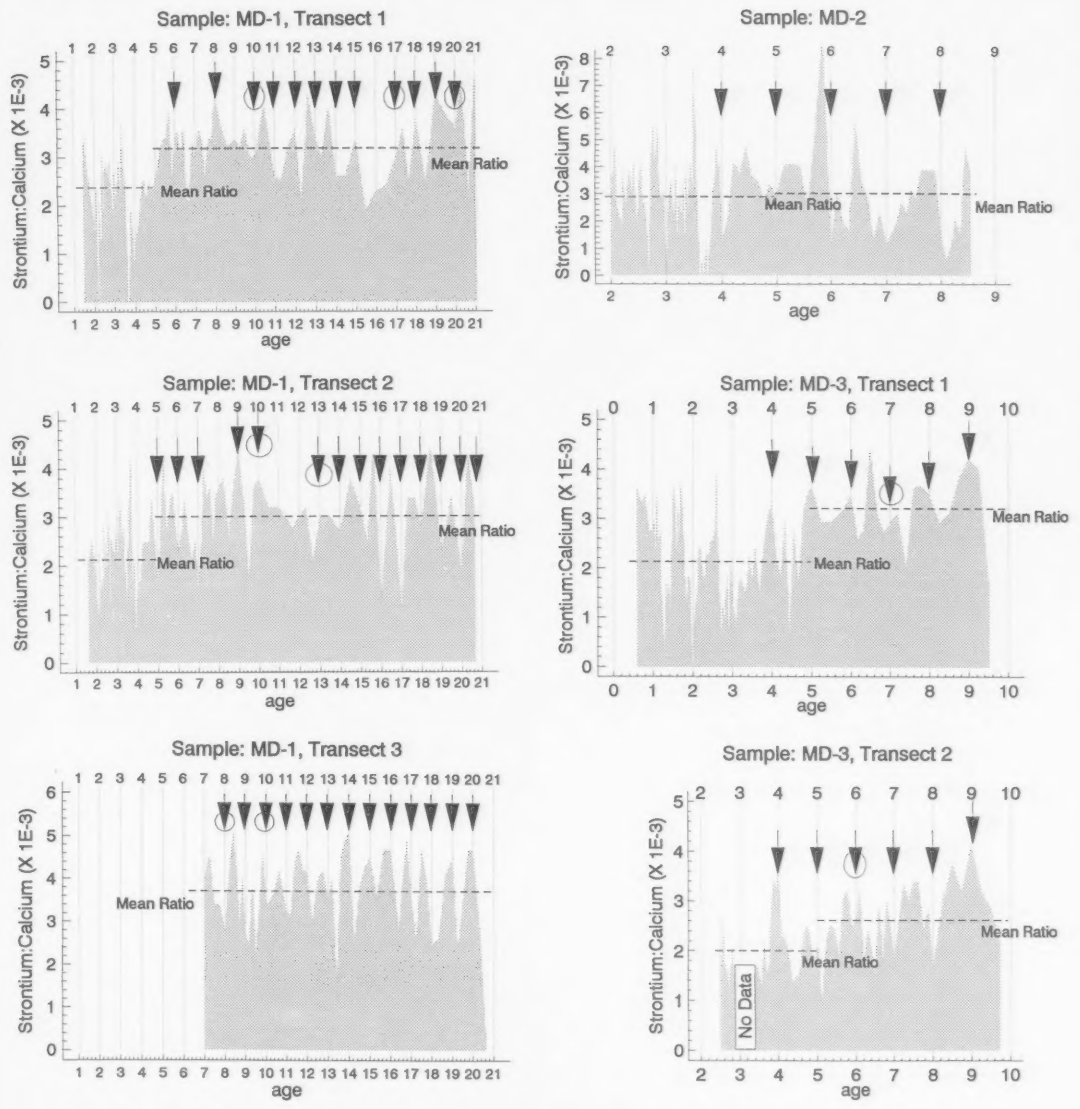


Figure 2

Transects of Sr/Ca ratios across annuli increments of Maryland striped bass *Morone saxatilis*. Mean ratios are plotted for ages <5 and ages ≥5 for each sample. See Table 3 for step sizes. Arrows indicate presumed freshwater excursions. Circled arrows indicate nadirs in ratios which were consistent with an annual cycle but did not coincide with annuli.

was 20 μm for both transects, did not significantly differ.

Despite the differences among transects, the overall trend in Chesapeake fish was a nadir in Sr/Ca ratio at or shortly after annuli that coincided with spring spawning runs (Merriman 1941, Robinson 1960). This trend occurred only in fish >4 years old. There was a significant increase in the overall Sr/Ca ratio in fish >5 years for two of three Chesapeake fish (Table 4).

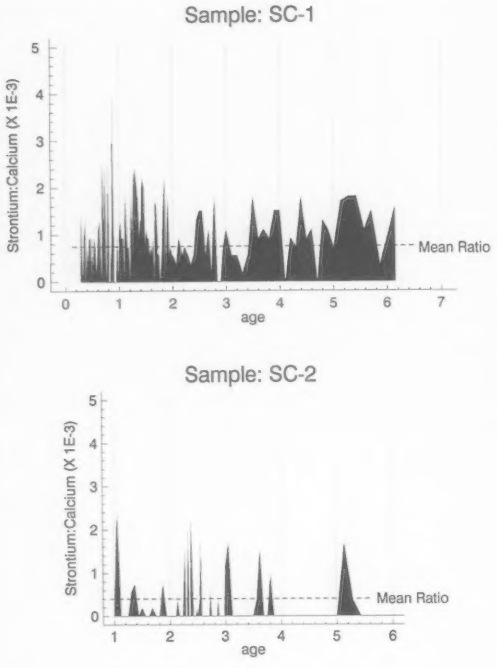


Figure 3
Transects of Sr/Ca ratios across annuli of adult female Santee-Cooper (SC) striped bass *Morone saxatilis*. Mean ratios are plotted across all ages.

Strontium was not detected in the Patuxent River juvenile striped bass otolith until it reached ~8 mm SL (Fig. 5). Because larvae less than this size tend to utilize freshwater nurseries (Houde and Rutherford 1992), this further verified that freshwater residence results in low levels of otolith Sr.

Discussion

Annulus formation

Rate and season of annulus formation in striped bass otoliths are critical to interpretation of the results on annual and seasonal changes in otolith microchemistry. Heidinger and Clodfelter (1987) validated the hypothesis of yearly annulus formation for young (<5 years old) striped bass. However, no directed research has documented the time of annulus formation in striped bass otoliths or scales despite their widespread use in fisheries (e.g., Beamish and McFarlane 1983). Several investigators have made the observation that annuli are not observed until spawning season in scales (Merriman 1941, Robinson 1960) and otoliths (M. White, S.C. Wildl. Mar. Resour., Bonneau SC 29431, pers. commun.). Based on these limited observations and the general trend of spring annulus formation in other North American temperate fishes, it was assumed that annular check formation occurred during or just prior to the spawning season (February–April).

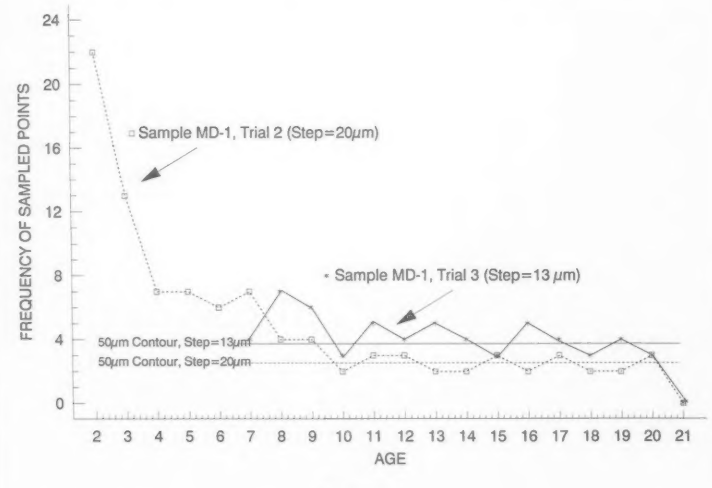


Figure 4
Number of sampled points between annuli checks at two step sizes. Contours for a hypothetical 50 μm annular increment are plotted at 13 and 20 μm step sizes.

Salinity effect on otolith microchemistry

Because Chesapeake samples had substantially higher Sr/Ca ratios than South Carolina samples, there appears to be a salinity effect on the ratio. This conclusion is further substantiated by the juvenile otolith that was examined and showed nondetectable Sr/Ca ratio during the early-larval period, a time when Chesapeake tributary larvae generally occur above the salt-wedge (Uphoff 1989, Houde and Rutherford 1992). Patterns in otolith Sr/Ca in adults were consistent with expected seasonal changes in ambient salinity. The range of ratios found for Chesapeake striped bass was similar to those found by Kalish (1989) for 12 marine species (Sr/Ca 0.0018

Table 4

Comparison of ratios between probed points <5 or ≥5 years. Significant differences ($p<0.001$) are shown by an asterisk.

		Age <5			Age ≥5			
Sample	Transect	$\bar{}$	SD	N	$\bar{}$	SD	N	t
MD-1	1	2.17	0.89	44	3.22	0.68	55	6.62*
	2	2.16	0.89	44	3.03	0.64	55	5.09*
MD-2	—	2.96	1.50	65	3.01	1.66	34	0.15
MD-3	1	2.15	0.93	78	3.20	0.67	22	4.95*
	2	2.01	0.62	35	2.61	0.70	35	3.78*

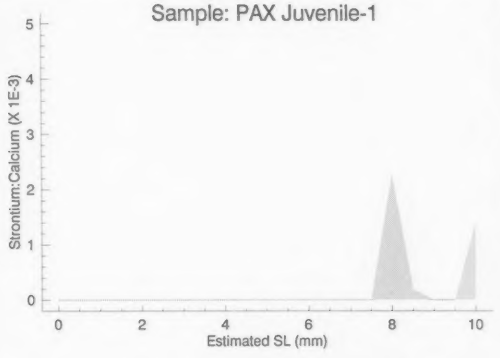


Figure 5

Transect of Sr/Ca ratios for the early-larval period from a juvenile striped bass *Morone saxatilis* sampled from the Patuxent River, 1991. Transect distance was converted to standard length using regression of standard length on otolith length for Potomac River striped bass larvae (Houde et al. 1992). Transect points were converted to larval lengths assuming a linear growth rate and constant otolith length:fish length relationship.

–0.0062) and 1 freshwater species (Sr/Ca 0.0005–0.0010).

Radtke (1984) and others (Townsend et al. 1989, Radtke et al. 1990) have shown an inverse relationship between temperature and otolith Sr/Ca ratio. If there were such an inverse relationship in adult striped bass otoliths, then ratios would increase during fall and winter and decrease during spring and summer, a pattern which would to some degree parallel the pattern seen for anadromous striped bass.

Kalish (1989, 1991) in recent directed research found no temperature relationship for otolith Sr/Ca ratio, and suggested that seasonal changes in fish physiology can cause incidental correlation between temperature and Sr/Ca ratios. Based on evidence for seasonal, growth, and age effects on Sr/Ca ratios, he postulated that during certain periods of active metabolism, Ca-binding proteins are more abundant in the serum which results in a higher relative fraction of free Sr available for deposition onto the otolith. If Sr/Ca ratios in the otolith are controlled by physiological processes alone, then a different pattern of Sr/Ca ratios would be expected compared with those observed for striped bass, i.e., Sr/Ca ratios would tend to rise in late-winter and early-spring during vitellogenesis but might also be high during periods of active growth. However, physiological effects such as sexual maturation and stress could explain both the increase in Sr/Ca ratio after the 5th annulus in Samples MD-1 and MD-3, and seasonal (subannular) patterns which varied among samples (e.g., the major peak which proceeded the 6th annulus in Sample MD-2; Fig. 2).

Although results exist for few species, the magnitude of the salinity effect found in this and other studies (Casselman 1982, Kalish 1989 and 1990) may be greater than differences expected due to physiological condition (Kalish 1989, 1991) and temperature alone (Radtke 1984, Townsend et al. 1989, Radtke et al. 1990). Similar to my findings, Kalish (1989, 1991) reported a three- to four-fold difference in Sr/Ca ratio between groups of young rainbow trout exposed to either freshwater or saltwater. Casselman (1982) reported a three-fold difference in Sr/Ca ratio between the marine and freshwater life-history phases of American eel. In laboratory-rearing studies on larval herring *Clupea harengus*, temperature effects resulted in no more than a two-fold difference in Sr/Ca ratios (Townsend et al. 1989, Radtke et al. 1990), although a complementary field study conducted by Townsend et al. (1989) showed that temperatures of 1–12°C had a four-fold effect on Sr/Ca ratio. Physiological condition has been associated with an approximate two-fold effect on Sr/Ca ratio in juvenile Australian salmon *Arripis trutta* (Kalish 1989).

A three-fold difference in Sr/Ca ratio in otoliths is consistent with the probable influence of ambient concentrations of Sr and Ca, since the Sr/Ca ratio is at least four times greater in saltwater than in freshwater (Casselman 1982, Radtke et al. 1988, Kalish 1989 and 1990). Further, Berg (1968) has shown substantially less physiological discrimination against Sr than Ca in scale formation, and Kalish (1989) shows excellent correspondence between otolith microchemistry and the chemical composition of endolymph that bathes the otolith. Therefore, ambient levels of Sr could be reflected in the otolith's microchemistry (Mugiya and Takahashi 1985, Kalish 1989) dependent upon the degree of physiological discrimination against Sr.

Otolith microchemistry and migratory history

The otolith microchemistry method offers great potential to address questions related to time of maturation and frequency of spawning. A distinct positive shift in Sr/Ca ratio at 5 years in samples MD-1 and MD-3 could be indicative of maturation or onset of coastal migration. Current estimates of age-at-maturation for Chesapeake population females indicate that <30% of females are mature by age 5 years (Maryland DNR 1991). Kohlenstein (1981) showed through a tagging study that the majority of female striped bass migrate by 5 years. Lack of a shift in MD-2 might indicate that this individual was a male or had a different migration history.

All Maryland striped bass samples showed annual peaks and valleys in Sr/Ca ratios. Based on a salinity effect, it can be inferred that valleys represent excursions into strontium-poor freshwater habitats. Assuming that large, mature adults venture into freshwater or low-salinity habitats to spawn, then spawning frequency can be estimated.

Precision error and spatial resolution of the electron microprobe analysis is critical in the proposed application of charting individual migratory histories. Precision errors were indicated by differences in Sr/Ca patterns and overall level between transects of the same sample (e.g., MD-3). Changing spatial resolution between measurements of 20 and 13 μm permitted greater resolution of seasonal (subannular) patterns. A more complete series of measures along a transect is taken at lower step sizes because gaps between measured points become narrower. This effect could explain variation in mean Sr/Ca levels among transects for the same sample. Alternatively, lack of agreement between transects could indicate machine precision limits in detecting Sr/Ca levels.

A decline in otolith growth rate with age also caused a decrease in spatial resolution (Fig. 4). At a 13 μm step size, four or five measurements were taken per annular increment in fish >7 years. Therefore, each measurement can correspond to several months of the fish's life. This would explain why nadirs in Sr/Ca ratio rarely approached zero after the 5th annulus. Tagging studies indicate that adult striped bass can migrate between freshwater and coastal habitats within a month (Mansueti 1961, Chapoton and Sykes 1961, Waldman et al. 1990). Peaks and nadirs observed in otolith Sr/Ca ratio may therefore represent temporally-averaged values. Laboratory verification studies are planned to gauge the spatial sensitivity of otolith microchemistry to resolve changes in ambient salinity.

Other life-history applications

An ingenious application of the Sr/Ca method to early-life-history consequences of anadromy was made by Kalish (1990). He was able to detect Sr in the core of salmonid otoliths (the earliest deposited material). Under the rationale that maternally-derived protein influenced offspring otolith microchemistry, it was possible to segregate offspring on the basis of whether they originated from eggs spawned by anadromous (high Sr/Ca) or nonanadromous (low Sr/Ca) females. In my study, a single striped bass juvenile of known anadromous parentage had no detectable Sr in the otolith core. In contrast to salmonid embryos and larvae, striped bass obtain relatively small amounts of maternal protein and lipids, and the period of endogenous feeding is considerably shorter. Also, the chorion of striped bass eggs is highly permeable; therefore, ambient concentrations of Sr could have a greater influence on otolith microchemistry.

Substantial variation in Sr/Ca ratio occurred for young adult (≤5 years old) Chesapeake fish. In all samples, values ranged below detection limits. Presumably these values represent excursions unrelated to spawning by young fish into freshwater systems. Freshwater and slightly saline environments in the upper reaches of Chesapeake Bay tributaries may serve as foraging grounds. Future research could analyze the duration and seasonality of freshwater habitation by fishes that reside in the Chesapeake Bay.

Further verification studies are needed to establish whether estuarine and marine phases can be distinguished using Sr/Ca ratios. Ratios tended to continuously increase following nadirs, and this pattern could indicate exposure to waters of increasing salinity. A verification study could be carried out by probing the last deposited otolith material (the edge) for Sr/Ca and relating that ratio to the salinity in which the striped bass was sampled in the field or through laboratory rearing studies (Kalish 1989, Townsend et al. 1989, Radtke et al. 1990). A key comparison will be that between samples from estuarine habitats (salinity 5–20 ppt) and marine habitats (≥32 ppt). Should differences be detectable between these groups, then it will be possible to infer detailed patterns of anadromy and related life-history traits.

Acknowledgments

Dr. Philip Picoli at the Central Facility for Microanalysis, University of Maryland, generously provided expertise and assistance with the electron microprobe. Drs. Ed Houde, John Kalish, and David Townsend gave useful criticisms on earlier versions of this manuscript.

Dr. John Dean made available samples of otoliths from South Carolina striped bass. Bunky's Charter Boat Service provided Chesapeake Bay samples. This research was supported by the U.S. Fish and Wildlife Service Emergency Striped Bass Study.

Citations

ASMFC (Atlantic States Marine Fisheries Commission)
1990 Amendment 4 to the Atlantic States Marine Fisheries Commission Interstate Striped Bass Management Report. Fish. Manage. Rep. 16, Versar Inc., Columbia, MD, 200 p.

Bagenal, T.B., F.J.H. Mackereth, and J. Heron
1973 The distinction between brown trout and sea trout by the strontium content of their scales. J. Fish Biol. 5:555–557.

Beamish, R.J., and G.A. McFarlane
1983 The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743.

Berg, A.
1968 Studies on the metabolism of calcium and strontium in freshwater fish. I. Relative contribution of direct and intestinal absorption. Mem. Ist. Ital. Idrobiol. 23:161–196.

Casselman, J.M.
1982 Chemical analysis of the optically different zones in eel otoliths. *In* Loftus, K.H. (ed.), Proc., 1980 North American eel conference, p. 74–82. Ont. Fish. Tech. Rep. Ser. 4, Ont. Minist. Nat. Resour.

Chapman, R.W.
1987 Changes in the population structure of male striped bass, *Morone saxatilis*, spawning in three areas of the Chesapeake Bay from 1984 to 1986. Fish. Bull., U.S. 85:167–170.

Chapoton, R.B., and J.E. Sykes
1961 Atlantic coast migration of large striped bass as evidence by fisheries and tagging. Trans. Am. Fish. Soc. 90:13–20.

Coutant, C.C.
1990 Microchemical analysis of fish hard parts for reconstructing habitat use: Practice and promise. *In* Parker, N.C., et al. (eds.), Fish marking techniques, p. 574–580. Am. Fish. Soc. Symp. 7, Bethesda.

Goldstein, J.I., D.E. Newberry, P. Echlin, D.C. Joy, C. Fiori, and E. Lifshin
1981 Scanning electron microscopy and x-ray microanalysis. Plenum Press, NY, 675 p.

Heidinger, R.C., and K. Clodfelter
1987 Validity of the otolith for determining age and growth of walleye, striped bass, and smallmouth bass in power cooling ponds. *In* Summerfelt, R.C. (ed.), Age and growth of fish, p. 241–251. Iowa State Univ. Press, Ames.

Houde E.D., and E.S. Rutherford
1992 Egg production, spawning biomass and factors influencing recruitment of striped bass in the Potomac River and Upper Chesapeake Bay. Final Rep. to Maryland Dep. Nat. Resour., Contract CB89-001-003. Univ. Maryland, Cent. Environ. Estuarine Stud., Ref. [UMCEES]-CBL 92-017, 313 p.

Ingram, B.L., and D. Sloan
1992 Strontium isotopic composition of estuarine sediments as paleosalinity-paleoclimate indicator. Science (Wash. DC) 255:68–72.

Kalish, J.M.
1989 Otolith microchemistry: Validation of the effects of physiology, age and environment on otolith composition. J. Exp. Mar. Biol. Ecol. 132:151–178.
1990 Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fish. Bull., U.S. 88:657–666.
1991 Determination of otolith microchemistry: Seasonal variation in the composition of blood plasma, endolymph and otoliths of bearded rockcod *Pseudophycis barbatus*. Mar. Ecol. Prog. Ser. 74:137–159.

Kinsman, D.J.J., and H.D. Holland
1969 The co-precipitation of cations with $CaCO_3$—IV. The co-precipitation of Sr^{2+} with aragonite between 16° and 96°C. Geochim. Cosmo. Acta. 33:1–17.

Kohlenstein, L.C.
1981 On the proportion of the Chesapeake Bay stock of striped bass that migrates into the coastal fishery. Trans. Am. Fish. Soc. 110:168–179.

Mansueti, R.J.
1961 Age, growth and movements of the striped bass, *Roccus saxatilis*, taken in size selective fishing gear in Maryland. Chesapeake Sci. 2:9–36.

Maryland DNR
1991 Investigation of striped bass in Chesapeake Bay. USFWS Federal Aid Project F-42-R-3, 1989–1990. Md. Dep. Nat. Resour., Tidewater Admin., 193 p.

Massman, W.H., and A.L. Pacheco
1961 Movements of striped bass in Virginia waters of the Chesapeake Bay. Chesapeake Sci. 2:37–44.

Merriman, D.
1941 Studies on the striped bass, *Roccus saxatilis*, of the Atlantic Coast. U.S. Fish Wildl. Serv. Fish. Bull. 50:1–77.

Mugiya, Y., and K. Takahashi
1985 Chemical properties of the saccular endolymph in the rainbow trout, *Salmo gairdneri*. Bull. Fac. Fish. Hokkaido Univ. 36:57–63.

Radtke, R.L.
1984 Formation and structural composition of larval striped mullet otoliths. Trans. Am. Fish. Soc. 113:186–191.

Radtke, R.L., R.A. Kinzie III, and S.D. Folsom
1988 Age at recruitment of Hawaiian freshwater gobies. Environ. Biol. Fishes 23:205–213.

Radtke, R.L., D.W. Townsend, S.D. Folsom, and M.A. Morrison
1990 Strontium: Calcium ratios in larval herring otoliths as indicators of environmental histories. Environ. Biol. Fishes 27:51–61.

Reed, S.J.B.
1975 Electron microprobe analysis. Cambridge Univ. Press, Cambridge, 400 p.

Robinson, J.B.
1960 The age and growth of striped bass (*Roccus saxatilis*) in California. Calif. Fish Game 46:279–290.

Secor, D.H., J.M. Dean, and E.H. Laban
1991 Manual for otolith removal and preparation for microstructure examination. Baruch Press, Univ. South Carolina, Columbia, 85 p.

Secor, D.H., J.M. Dean, T.A. Curtis, and F.W. Sessions
1992 Effect of female size and propagation methods on larval production at a South Carolina striped bass (*Morone saxatilis*) hatchery. Can. J. Fish Aquat. Sci. 49:1778–1787.

Setzler-Hamilton, E.M., and L.W. Hall Jr.
1991 Striped bass *Morone saxatilis*. *In* Funderburk, S.L., et al. (eds.), Habitat requirements for Chesapeake Bay living resources, 2d ed., p. 13-1–13-31, plus maps. Living Resources Subcommittee, Chesapeake Bay Program, Annapolis.

Townsend, D.W., R.L. Radtke, M.A. Morrison, and S.D. Folsom
1989 Recruitment implications of larval herring overwintering distributions in the Gulf of Maine, inferred using a new otolith technique. Mar. Ecol. Prog. Ser. 55:1–13.

Uphoff, J.H.
1989 Environmental effects on survival of eggs, larvae and juveniles in the Choptank River, Maryland. Trans. Am. Fish. Soc. 118:251–263.

Vladykov, V.D., and D.H. Wallace
1952 Studies of striped bass *Roccus saxatilis* (Walbaum) with special reference to the Chesapeake Bay region during 1936–1938. Bull. Bingham Oceanogr. Collect., Yale Univ. 14(1):132–177.

Waldman, J.R., D.J. Dunning, Q.E. Ross, and M.T. Mattson
1990 Range dynamics of Hudson River striped bass along the Atlantic coast. Trans. Am. Fish. Soc. 119:910–919.

Wilson, C.A. et al.
1987 Glossary. *In* Summerfelt, R.C., and G.E. Hall (eds.), Age and growth of fish, p. 527–530. Iowa State Univ. Press, Ames.

Leatherback turtle captured by ingestion of squid bait on swordfish longline

Robert A. Skillman
George H. Balazs

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396

The leatherback turtle *Dermochelys coriacea* is the only species of the family Dermochyidae. The other six extant marine turtles are hard-shelled members of the family Cheloniidae. The leatherback inhabits the pelagic marine environment, apparently only leaving to breed in coastal waters. With recorded dives to 475 m, it is among the world's deepest-diving vertebrates (Eckert et al. 1986). With weights up to 916 kg, it is the world's largest turtle (Eckert and Luginbuhl 1988). The leatherback is listed as endangered under the U.S. Endangered Species Act, the International Union for Conservation of Nature, and the Convention on International Trade in Endangered Species. Consequently, fishery interactions involving the leatherback are of concern. This paper reports an interaction with longline gear while fishing for swordfish.

Leatherbacks ingest and become entangled in marine debris (Balazs 1985), and they are taken by operative fishing gear (Nishemura and Nakahigashi 1990). Entanglement has been reported with lobster pot lines (Lazell 1976), drift nets (Balazs 1982, Wetherall et al. In Press); pelagic longline (Witzell 1984, Tobias 1991); gillnets (Margaritoulis 1986); and swordfish *Xiphias gladius* tangle nets (Frazier and Brito Montero 1990). Interactions with tuna and swordfish longline fishing have involved entanglement and foul-hooking, particularly with the leatherback's long flippers (Honolulu Star-Bulletin 1935, Witzell 1984, Dollar 1991, Tobias 1991, USFWS 1969). In the Hawaii swordfish fishery, sightings of leatherbacks and reported interactions are not rare, particularly in the area of the seamounts above the Northwestern Hawaiian Islands (Robert Dollar, NMFS Honolulu Lab., pers. commun.). It is not uncommon for leatherbacks to become entangled in driftnets set north of Hawaii between 30° and 45°N. However, virtually nothing is known about their overall distribution, abundance, and life history including stock structure (Wetherall et al., In press). The nearest colonies of nesting leatherbacks occur in the eastern Pacific along the coast of Mexico and Costa Rica and in the western Pacific in peninsular Malaysia. To our knowledge, ingestion of baited hooks has not been reported in the literature.

Leatherbacks are known to feed on gelatinous, pelagic animals. These include the medusa of sychozoan coelenterates (true jellyfish) (Bleakney 1965, Brongersma 1969) and hydrozoan coelenterates (Portuguese man-of-war *Physalia arethusa*) (Bacon 1970). Davenport (1988) and Davenport and Balazs (1991) have suggested the potential importance of bioluminescence in the predation of free-swimming colonial tunicates (pyrosomas) by leatherbacks during the night or on deep dives. Neither fish (tuna bait) nor squid (swordfish bait) have been cited in the literature as prey of leatherbacks. Accordingly, Witzell (1984) stated that leatherbacks are not likely to be taken on a baited hook.

The present paper presents documentation of a leatherback captured after ingesting squid bait on swordfish longline gear. The chemical light sticks used to attract swordfish may have attracted the leatherback to the gear.

On 24–25 January 1991, while experimental longline fishing operations were being conducted for swordfish from the NOAA research ship *Townsend Cromwell*, a leatherback turtle was hooked and released alive at lat. 26°58.3′N, long. 168° 53.5′W. The turtle swam vigorously while being hauled next to the research vessel and after being released. The hook line could be seen coming from the turtle's mouth, but the exact location of the hook was not apparent. No blood or external injuries were apparent. A tree branch lopper on the end of an extendable fiberglass pole was used to cut the hook line a few centimeters from the turtle's mouth. The estimated carapace length of the turtle was 170 cm. The turtle was too large to haul on board, and the prevalence of sharks, including blue shark *Prionace glauca*, made it impossible to enter the water for accurate measurement or tagging. Other site specifics included the following: 2400 m bottom depth, 21.4°C sea surface-water temperature, 18.9°C air temperature, 150–180 cm sea swells, northeasterly trade winds at 15 kn, and approximate depth of the upper mixed layer at 85 m.

Details of the set and gear are as follows. The longline gear consisted of ~16 km of 4.0 or 3.2 mm monofilament main line suspended with floats every 3 hook lines. The gear, with 206 hooks, was set on 24

Manuscript accepted 6 August 1992.
Fishery Bulletin, U.S. 90:807–808 (1992).

January 1991 starting at lat. 27°01.720′N, long. 168°56.153′W, in the vicinity of an unnamed seamount some 940 km east of Midway Is. and 150 km north-northeast of Raita Bank, Northwestern Hawaiian Is. The gear was hauled on 25 January beginning at lat. 26°59.094′N, long. 168°57.810′W. The turtle was taken on the first hook of a 3-hook basket located about mid-set. This hook was set at 1818h and hauled at 0907h the next day, for a soak time of 14h 49 min. Because the hook timer (a 7.5×3 cm cylinder of clear plastic resin with an embedded clock chip; Somerton et al. 1988) on that line was lost, an estimate of the time of hooking is not available. The hook timer on the second hook-line, with full bait remaining, was set off at 0511h; the hook timer on the first hook of the previous basket, with the bait missing, was set off at 0159h. The float lines, made of polypropylene rope, were 9 m long. The hook droppers, made of 2.1 mm monofilament, were 13 m long with a 60 g weighted swivel 4 m from the hook. Thus, the depth of hook 1 was nominally ~22 m, unless altered by currents, since the first hook-line of each basket was attached within 3 m of the float. Green, 12 h chemical light sticks were placed ~2 m above each of the 206 hooks (the light sticks still glowed weakly at the time of hauling). Each hook was baited with a whole, previously-frozen Argentinean squid (*Illex* sp.), weighing ~0.34 kg.

While entanglement of leatherbacks in pelagic longline and other gears has been described, ours is apparently the first report of a hook and bait being eaten. Chemical light sticks used on swordfish longline may impose an added hazard for leatherbacks by simulating natural prey. The magnitude of the take, the level of mortality or serious injury, and the impact on the leatherback stock are unknown. Additional data on the take by pelagic fisheries as well as information on leatherback feeding habits, stock structure, and population dynamics would be needed to evaluate the impact of the take.

Citations

Bacon, P.R.
1970 Studies on the leatherback turtle *Dermochelys coriacea* (L.), in Trinidad, West Indies. Biol. Conserv. 2:213–217.

Balazs, G.H.
1982 Driftnets catch leatherback turtles. Oryx 16:428–430.
1985 Impact of ocean debris on marine turtles: Entanglement and ingestion. *In* Shomura, R.S., and H.O. Yoshida (eds.), Proceedings, Workshop on the fate and impact of marine debris, 27–29 November 1984, Honolulu, p. 387–429. NOAA Tech. Memo. NMFS-SWFC-54, NMFS Honolulu Lab.

Bleakney, J.S.
1965 Reports of marine turtles from New England and eastern Canada. Can. Field-Nat. 19:120–128.

Brongersma, L.D.
1969 Miscellaneous notes on turtles, IIB. Proceedings, K. Ned. Akad. Wet. Ser. C, Biol. Med. Sci. 72:90–102.

Davenport, J.
1988 Do diving leatherbacks pursue glowing jelly? Br. Herpetol. Soc. Bull. 24:20–21.

Davenport, J., and G.H. Balazs
1991 'Fiery bodies'—Are pyrosomas an important component of the diet of leatherback turtles? Br. Herpetol. Soc. Bull. 37:33–38.

Dollar, Robert A.
1991 Summary of swordfish longline observations in Hawaii, July 1990–March 1991. Admin. Rep. H-91-09, NMFS Honolulu Lab., 13 p.

Eckert, K.L., and C. Luginbuhl
1988 Death of a giant. Mar. Turtle Newsl. 43:2–3.

Eckert, S.A., D.W. Nellis, K.L. Eckert, and G.L. Kooyman
1986 Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during internesting intervals at Sandy Point, St. Croix, U.S. Virgin Islands. Herpetologica 42(3):381–388.

Frazier, J.G., and J.L. Brito Montero
1990 Incidental capture of marine turtles by the swordfish fishery at San Antonio, Chile. Mar. Turtle Newsl. 49:8–13.

Honolulu Star-Bulletin
1935 [Photograph with a caption indicating a 200 kg leatherback turtle was found entangled in the line and hooks of a sampan, a Japanese-style fishing boat probably using longline gear.] Honolulu Star-Bulletin, 8 April 1935, p. 3.

Lazell, J.D. Jr.
1976 This broken archipelago. Cape Cod and the islands, amphibians and reptiles. Demeter Press Book, Gräfelfing, Germany, p. 191.

Margaritoulis, D.N.
1986 Captures and strandings of the leatherback sea turtle, *Dermochelys coriacea*, in Greece (1982–1984). J. Herpetol. 20(3):471–474.

Nishemura, W., and S. Nakahigashi
1990 Incidental capture of sea turtles by Japanese research and training vessels: Results of a questionnaire. Mar. Turtle Newsl. 51:1–4.

Somerton, D.A., B.S. Kikkawa, and C.D. Wilson
1988 Hook timers to measure the capture of individual fish. Mar. Fish. Rev. 50(2):1–5.

Tobias, W.
1991 Incidental catch a continuing problem in the Mediterranean. Mar. Turtle Newsl. 51:10–12.

USFWS (U.S. Fish & Wildlife Service)
1969 Cruise report, USFWS ship *Townsend Cromwell*, cruise 44. USFWS Hawaii Area Biol. Lab., 4 p. [Avail. NMFS Honolulu Lab.]

Wetherall, J.A., G.H. Balazs, R.A. Tokunaga, and M.Y.Y. Yong
In press Bycatch of marine turtles in North Pacific high-seas driftnet fisheries and impacts on the stocks. *In* Proc., Int. North Pac. Fish. Comm., Nov. 4–6, 1991, Tokyo.

Witzell, W.N.
1984 The incidental capture of sea turtles in the Atlantic U.S. Fishery Conservation Zone by the Japanese tuna longline fleet, 1978–81. Mar. Fish. Rev. 46(3):56–58.

Reproductive biology of the swordfish *Xiphias gladius* in the Straits of Florida and adjacent waters

Ronald G. Taylor
Michael D. Murphy

Florida Marine Research Institute, Department of Natural Resources
100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095

The swordfish *Xiphias gladius* Linnaeus inhabits all tropical, subtropical, and temperate oceans of the world, including the Mediterranean Sea and the Gulf of Mexico. In the western Atlantic, it is found from Newfoundland to Argentina (Palko et al. 1981, Nakamura 1985). Swordfish occur in the Florida Straits at all times of the year. Prior to 1970, swordfish were pursued primarily by recreational fishermen. During the 1970s, the fishery in Florida attracted displaced Cuban-Americans and New England longline fishermen, and by 1980 commercial landings from the east coast of Florida had reached nearly 1500 mt (Berkeley and Irby 1982).

Little is known about the reproductive biology of swordfish in the western Atlantic. Ovchinnikov (1970) and Berkeley and Houde (1980) reported contradictory findings on male and female sizes-at-maturity. Wilson (1984) reported that males mature at younger ages than do females in the U.S. south Atlantic. Descriptions of swordfish spawning season and spawning grounds have been based on the temporal and areal distribution of infrequently-collected larvae and juveniles (Arata 1954, Tibbo and Lauzier 1969, Markle 1974, Grall et al. 1983). Our research objectives were to determine the size- and age-at-maturity, spawning season, and approximate spawning grounds of swordfish in the Straits of Florida and adjacent waters. Data were collected as part of a joint Florida Marine Research Institute and University of Miami investigation of the fishery and biology of the swordfish. Samples gathered during this research have been used to develop a method to determine the ages of swordfish and to describe their growth (Berkeley and Houde 1984).

Methods and materials

Swordfish were sampled from recreational and commercial catches made off southeast Florida (Fig. 1) from June 1977 through November 1980. Each year most of the collections were made April through September. Samples were taken at least once each month over the 2.5 yr sampling period, except in December when no samples were taken either year. Because of the varied conditions of landed swordfish, a variety of length measurements (to the nearest cm) were taken: total length (TL), distance from the tip of the bill to the midpoint of the line connecting the distal edges of the caudal-fin lobes; fork length (FL), from the tip of the bill to the distal end of the central ray of the caudal fin; lower jaw to fork length (LJFL), from the tip of the lower jaw to the distal end of the central ray of the caudal fin; eye to fork length (EFL), from the posterior margin of the eye's bony orbit to the distal end of the central ray of the caudal fin; and trunk length (TRNKL), from the posterior margin of the gill cavity to the point of least circumference of the caudal peduncle. Lower jaw to fork length is used throughout this paper unless otherwise noted. For fish measured only for TL, FL, EFL, or TRNKL, LJFL was estimated using the appropriate regression equation (Table 1). Whole weight (W) was determined to the nearest pound and converted to kilograms for our analyses. Portions of ovaries and testes were collected and preserved in Davidson's fixative (Humason 1972). Whole gonads, macroscopically judged ripe or mature based on the presence of transparent eggs, were preserved and then weighed to the nearest gram.

Swordfish maturity was described using histological features to define gonadal development. Subsamples of preserved gonads were embedded in paraffin, sectioned at 6 μm, stained with Mayer's haematoxylin and eosin, and mounted for microscopic examination. Swordfish were assigned to one of eight developmental classes following Murphy and Taylor (1990) and based on the appearance of histological features described by Grier (1981) for males and Wallace and Selman (1981) for females. These developmental classes and the mean observed oocyte diameters are (1) Immature, <20 μm; (2) Developing, 71 μm; (3) Maturing, 160 μm; (4) Mature, 434 μm; (5) Gravid, 723 μm; (6) Spawning/Partially Spent, 823 μm; and (7) Spent, 181 μm. The relationship between swordfish maturity and length was described for each sex using maturity data for fish grouped into 10 cm size-classes. A logistic distribution function was fit to the percentages of mature fish ($\geq$Class 4) and the midpoints of their size-classes (Saila et al. 1988) in order to predict a maturity schedule. A similar distribution function was generated for maturity against age.

Manuscript accepted 2 July 1992.
Fishery Bulletin, U.S. 90:809–816 (1992).

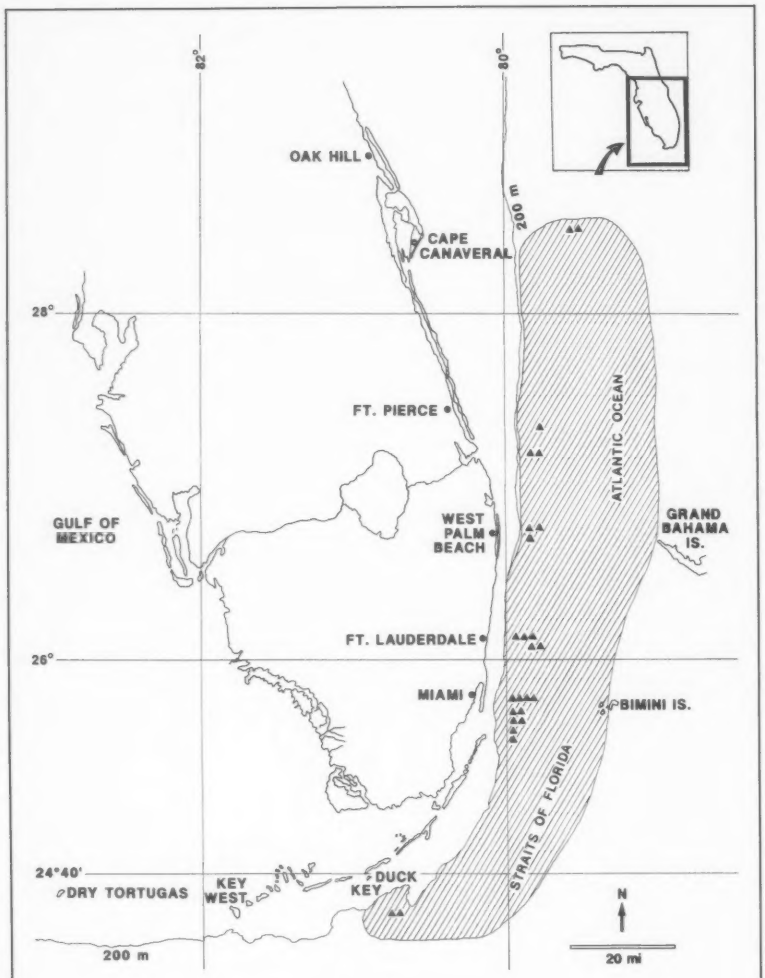


Figure 1

Areal extent of sampling locations (shaded area) off southeast Florida during June 1977–November 1980. Triangles indicate where female swordfish *Xiphias gladius* were found with histological evidence for recent (postovulatory follicles) or imminent (hydrated oocytes) spawning (see "Methods and materials").

Table 1

Linear regressions of lower jaw to fork length (LJFL) on total length (TL), fork length (FL), eye to fork length (EFL), or trunk length (TRNKL); and nonlinear regressions of whole weight (W) on lower jaw to fork length and LJFL on W, for swordfish *Xiphias gladius* off southeast Florida (regression analysis, SAS 1982).

Equation	N	Range	r^2
LJFL = −6.03 + 0.662(TL)	401	32–432 cm TL	0.982
LJFL = −5.51 + 0.714(FL)	100	30–396 cm FL	0.983
LJFL = 8.89 + 1.076(EFL)	316	68–249 cm EFL	0.995
LJFL = 15.71 + 1.402(TRNKL)	324	18–189 cm TRNKL	0.987
$W = 1.050 \times 10^{-5}$ LJFL$^{3.038}$	127	27–281 cm LJFL	0.973
LJFL = 48.58W$^{0.305}$	127	0.090–168.0 kg W	0.980

Ages for the swordfish that comprise this data set were determined by Berkeley and Houde (1984), who counted unvalidated age marks found on thin-sections of the second anal-fin spine.

Temporal differences in mean oocyte diameters were used to define spawning season. To determine mean oocyte diameter for each individual, 100 oocytes in a common lamella were measured with an ocular micrometer. Mean oocyte diameters were calculated for all collections in a given month and plotted to examine monthly changes. The distribution of oocyte diameters was also examined within individuals to determine whether swordfish undergo multiple spawns or a single spawn each year.

We used the distribution of swordfish captured in near-term spawning condition to delimit their spawning grounds off southeast Florida. Histological features indicative of recent or imminent spawning included postovulatory follicles and hydrated oocytes (DeMartini and Fountain 1981, Hunter and Macewicz 1985). For a variety of fishes, it has been found that oocytes hydrate during the late-afternoon or evening just prior to spawning (*Serrifus politus*, DeMartini and Fountain 1981; *Engraulis mordax*, Hunter and Macewicz 1985; *Cynoscion nebulosus*, Brown-Peterson et al. 1988; *Sciaenops ocellatus*, Fitzhugh et al. 1988). Postovulatory follicles are identifiable only for a short time. Following spawning, they are rapidly absorbed (within 6 h for *Callionymus enneactis*, Takita et al. 1983) and quickly become indistinguishable from other atretic structures (within 2 d in *Engraulis mordax*, Hunter and Macewicz 1985).

Batch fecundity was estimated gravimetrically from counts of ova >750 μm diameter in a 2–3 g portion from the midsection of each preserved ovary (n 7).

Results

Sex and length data were collected from 554 swordfish: 211 females 72–281 cm, and 343 males 82–235 cm. Gonads were available for histological processing from 295 fish (133 males and 162 females), of which 149 were ascribed ages.

Table 2

Observed and predicted percentages of mature (≥Class 4, see "Methods and materials") swordfish *Xiphias gladius* in 10 cm LJFL length intervals. Predicted percentages were calculated from logistic distribution functions fit to observed maturity data (see "Results"). Numbers in parentheses are numbers of fish examined.

Lower jaw to fork length interval midpoint (cm)	Male		Female	
	Observed %(*N*)	Predicted %	Observed %(*N*)	Predicted %
80			0(1)	0
90	0(3)	11	0(2)	0
100	33(3)	24	0(7)	0
110	46(11)	45	0(17)	0
120	64(11)	69	0(19)	1
130	90(10)	85	0(14)	3
140	96(24)	94	0(8)	5
150	93(14)	98	0(2)	10
160	100(11)	99	0(3)	18
170	100(14)	100	50(4)	30
180	100(11)	100	60(10)	47
190	100(8)	100	56(16)	64
200	100(6)	100	71(14)	78
210	100(5)	100	75(16)	87
220	100(1)	100	100(10)	93
230	100(1)	100	100(6)	97
240			100(3)	98
250			100(5)	99
260			100(2)	100
270				
280			100(3)	100

Table 3

Observed and predicted percentages of mature (≥Class 4, see "Methods and materials") swordfish *Xiphias gladius* by assigned age group (ages from Berkeley and Houde 1984). Predicted percentages were calculated from logistic distribution functions fit to observed maturity data (see "Results"). Numbers in parentheses are numbers of fish examined.

Age (years)	Male		Female	
	Observed %(*N*)	Predicted %	Observed %(*N*)	Predicted %
0	0(1)	4		
1	30(10)	29	0(13)	0
2	80(10)	79	0(18)	1
3	93(14)	97	0(6)	5
4	92(12)	100	18(11)	14
5	100(12)	100	38(8)	37
6	100(8)	100	60(10)	66
7			100(3)	87
8	100(2)	100	83(6)	96
9			100(4)	99
10			100(1)	100

Male swordfish mature at a smaller size and younger age than do females. Males begin to mature at ~100 cm at age 1 (Tables 2, 3). The proportion of mature males in our samples increased rapidly thereafter, and all males were mature by 160 cm or age 5. In contrast, the smallest mature females were ~170 cm or age 4, and all females were mature by 220 cm or age 9. The predicted length at 50% maturity, based on the fit of logistic distribution functions to the percentage mature within size-classes, was significantly less (approximate t-test, Sokal and Rohlf 1981; t' 36.5, df 33, $P<0.001$) for males (112 cm) than for females (182 cm). Likewise, age at 50% maturity was significantly younger for males (1.4 yr) than for females (5.5 yr; t' 17.7, df 16, $P<0.001$). The logistic distribution functions for maturity by size-class and age fit observed data well (Tables 2, 3) and are as follows:

Males:

$$\%\ \text{Mature} = 1/(1+e^{(-0.0976(\text{LJFL}-112))}) \quad (n\ 15,\ r^2\ 0.980)$$

$$\%\ \text{Mature} = 1/(1+e^{(-2.223(\text{AGE}-1.40))}) \quad (n\ 8,\ r^2\ 0.990)$$

Females:

$$\%\ \text{Mature} = 1/(1+e^{(-0.0690(\text{LJFL}-182))}) \quad (n\ 20,\ r^2\ 0.966)$$

$$\%\ \text{Mature} = 1/(1+e^{(-1.234(\text{AGE}-5.45))}) \quad (n\ 10,\ r^2\ 0.976).$$

Swordfish from southeast Florida waters demonstrate group-synchronous oocyte maturation (*sensu* Wallace and Selman 1981). This pattern of oocyte development is characterized by the presence of at least two distinct groups of dissimilar-sized oocytes during the spawning season. Ovaries from all swordfish in our samples contained a dominant group of oocytes <200 μm diameter (Fig. 2). All oocytes within Maturing ovaries (Class 3) were <200 μm, although lipid deposition suggests preparation for active vitellogenesis. Mature ovaries (Class 4) contained an additional distinct group of vitellogenic oocytes at 200–600 μm. A third group of oocytes, 600–1100 μm, were present only in Gravid and Spawning/Partially Spent fish (Classes 5 and 6). This largest

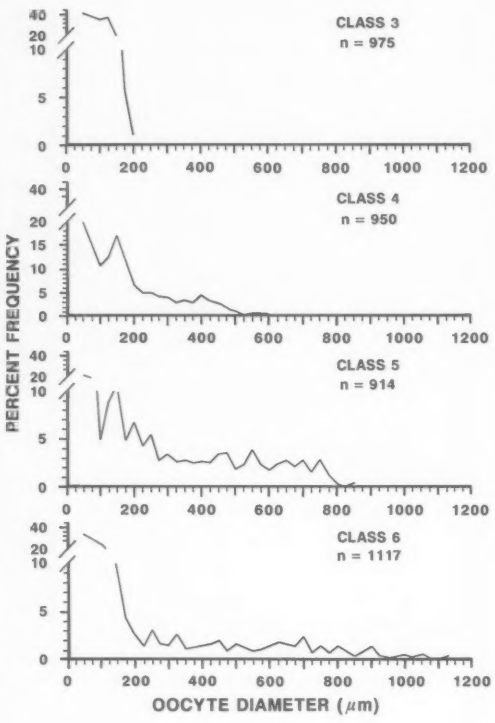


Figure 2

Percent frequency of oocyte diameters for swordfish *Xiphias gladius* collected during the spawning season off southeast Florida with ovaries in Classes: (3) Maturing, (4) Mature, (5) Gravid, and (6) Spawning/Partially Spent (see "Methods and materials").

group of oocytes proceeds through final maturation and represents the clutch (Wallace and Selman 1981) to be shed during the next spawning event.

The reproductive season for swordfish is protracted. Mature or actively spawning females were found during each month sampled, except January. Gravid or actively spawning males were found during all months sampled (Fig. 3). The greater numbers of spawning fish taken from late-spring to midsummer suggests increased spawning activity then. In addition, mature swordfish show a sharp increase in their maximum oocyte diameters to >800 μm beginning in April and extending through July, indicating peak spawning activity then (Fig. 4).

Histological features (postovulatory follicles and hydrated oocytes) provide evidence for active swordfish spawning off the Atlantic coast of Florida from about 24°40′N in the Straits of Florida southwest of Duck Key to about 28°25′N just west of Cape Canaveral (Fig. 1). The easternmost location where fish in spawning condition were collected was 16 km east of Grand Bahama Island at 480 m depth. About 25% of the fish collected at the westward extent of our sampling area (about the 200 m contour) exhibited evidence of recent or imminent spawning.

There was a preponderance of smaller males in our spring and summer samples. Overall, males significantly dominated the catch (345 M:216 F; χ^2 29.7, df 1, $P<0.001$); although at sizes >200 cm, females significantly outnumbered males (22 M:67 F; χ^2 22.8, df 1, $P<0.001$). There was no histological indication of hermaphroditism throughout the 72–281 cm length range. During spring and summer, males were dominant (266 M:152 F; χ^2 31.1, df 1, $P<0.001$); but during the fall and winter there was no significant difference in abundances of sexes (79 M:64 F; χ^2 1.6, df 1, $P>0.05$).

The batch fecundity of the seven swordfish sampled was 1.4–4.2 million eggs for swordfish 177–281 cm and 69–268 kg (Table 4). There was no obvious relationship between our estimates of batch fecundity and length or weight. The correlation coefficients between batch fecundity and length (r 0.21) and between batch fecundity and weight (r 0.64) were not significantly different from zero (table of critical values for correlation coefficients, df 5, $P>0.05$, Rohlf and Sokal 1981).

Discussion

Sizes-at-maturity have been reported for swordfish in the Atlantic and Pacific Oceans and Mediterranean Sea (Ovchinnikov 1970, Berkeley and Houde 1984, DeMetrio et al. 1989). However, in these reports maturity was determined by visual inspection of gonads, and no explanations were given as to whether the sizes reported were for first maturity or for 50% maturity. Berkeley and Houde (1984) reported that western Atlantic male and female swordfish mature at ~21 kg and 74 kg, respectively. This corresponds closely to the lengths-at-50%-maturity we present for swordfish off southeast Florida. Using equations in Table 1, we determined 50% maturity of males at 18 kg (112 cm LJFL converted to whole weight) and 50% maturity of females at 77 kg (182 cm). Ovchinnikov (1970) reported that male swordfish "reach maturity" in the Atlantic at about 100 cm (type of measure unknown). However, he reported a smaller size-at-maturity for females (70 cm). DeMetrio et al. (1989) reported that male swordfish in the eastern Mediterranean Sea first begin to mature at 82–105 cm LJFL and that nearly all are mature when >135 cm. Females

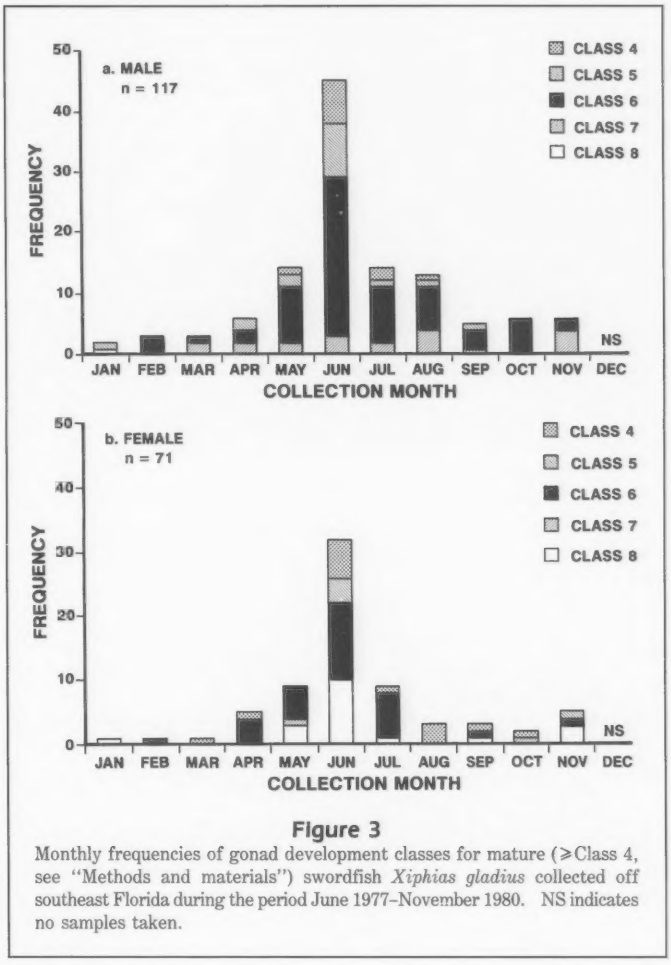


Figure 3

Monthly frequencies of gonad development classes for mature (≥Class 4, see "Methods and materials") swordfish *Xiphias gladius* collected off southeast Florida during the period June 1977–November 1980. NS indicates no samples taken.

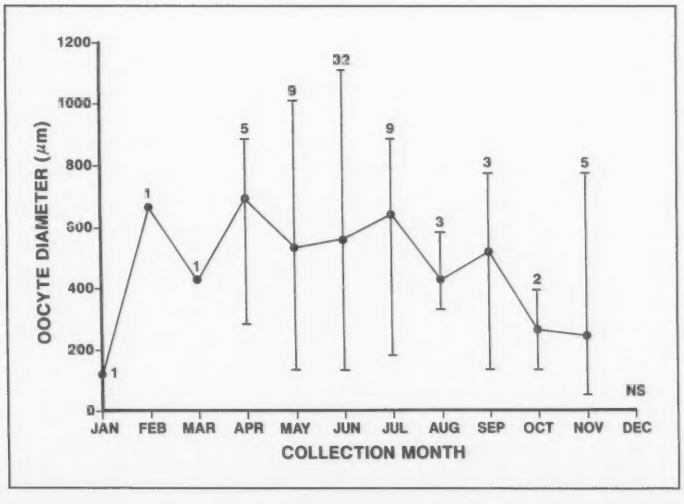


Figure 4

Monthly mean and range (vertical bars) of individual mean oocyte diameters for all mature (Class ≥4) swordfish *Xiphias gladius* collected off southeast Florida during the period June 1977–November 1980. Numbers indicate sample size; NS indicates no samples taken.

in the Mediterranean first reach maturity at 106–135 cm LJFL, and about 50% of the females >135 cm are mature. This is in contrast to our findings that the smallest mature females off Florida were ~170 cm LJFL and that 50% of females reached maturity when ~180 cm.

Female swordfish from the Pacific Ocean mature at sizes comparable to or somewhat smaller than those in the western Atlantic. From 1949 to 1958, Yabe et al. (1959) examined 372 female swordfish taken by a Japanese longline fleet in the North Pacific. They found only five mature females and suggested that females in the North Pacific begin to mature at 150–170 cm EFL (170–192 LJFL). Kume and Joseph (1969) concluded that female swordfish off California begin to mature at slightly smaller sizes, 139 cm EFL (158 cm LJFL), and are regularly found in ripe condition at >170 cm (192 cm LJFL).

The ages-at-maturity we estimated for male (1.4 yr) and female (5.5 yr) swordfish off southeast Florida are somewhat younger and older, respectively, than those determined for male and female swordfish collected farther north in the U.S. South Atlantic. From a relatively small sample collected off North Carolina and South Carolina, Wilson (1984) determined that males mature between ages 2 and 3 (15 mature males of 24 examined). Females mature between ages 4 and 5 (2 mature females of 18 examined). Although Wilson (1984) relied on a different technique (thin-sectioned otoliths) than did our study (thin-sectioned spines) to determine swordfish ages, he compared the two aging techniques and found they provided similar swordfish ages through at least age 5.

Female swordfish mature at a younger age in the eastern Mediterranean Sea than in the western Atlantic or Pacific Oceans. In the eastern Mediterranean,

Table 4

Estimates of batch fecundity for seven swordfish *Xiphias gladius* sampled off southeast Florida, including lower jaw to fork length, age (Berkeley and Houde 1984), whole weight, gonad development class, and oocyte diameters.

Batch fecundity (millions)	Lower jaw to fork length (mm)	Age (yr)	Whole weight (kg)	Gonad class	Hydrated oocyte size		
					N	$\bar{x}$	range
1.398	256	6	107	6	1754	0.98	0.83–1.16
2.814	252	9	223	6	1288	1.04	0.75–1.14
2.836	207	8	116	6	1656	1.56	1.30–1.77
3.071	177	—	69	6	2036	1.55	1.33–1.73
3.125	233	—	170	6	2121	1.35	1.17–1.57
4.220	281	—	268	6	2912	1.54	1.34–1.68
4.220	256	9	210	6	1232	1.11	0.96–1.23

DeMetrio et al. (1989) found mature female swordfish as young as age 2, with most mature by age 3. However, Yabe et al. (1959) suggested that female swordfish in the North Pacific mature at age 5 or 6. This is in agreement with our age-at-50%-maturity for females (5.5 years). Although we found no information on maturation of male swordfish from the Pacific, most male swordfish in the eastern Mediterranean reach maturity by age 2 (DeMetrio et al. 1989), again similar to our findings off southeast Florida.

The observed protracted spawning of swordfish off southeast Florida, with peak activity during April through July, agrees with reported spawning seasons determined from temporal changes in the abundance of larvae and juveniles. Taning (1955) reported that spawning off Florida and elsewhere in the North Atlantic occurs throughout the year, with peak larval abundances during February through April. The temporal distribution of larval abundance in the western North Atlantic suggests that swordfish spawn during December through September, with a peak in April (Arata 1954, Markle 1974, Grall et al. 1983). Off the coast of southern California, gonads of female swordfish are inactive from late-August through mid-November (Weber and Goldberg 1986). This period of inactivity coincides with low mean oocyte diameters of swordfish in the western Atlantic (Fig. 4), suggesting that swordfish in the eastern Pacific and western Atlantic may have similar annual spawning seasons.

Two histological features present in ovarian tissue—hydrated oocytes and postovulatory follicles—provided evidence that female swordfish spawn off the coast of southeast Florida between the Florida Keys and Cape Canaveral. The presence of hydrated oocytes indicates an imminent spawn, certainly within 12 h. Young postovulatory follicles found in many female swordfish provide evidence that spawning occurred within 24 h of capture. Further, short-term studies of the movement of swordfish, using acoustic tags, have shown that fish that were likely mature (70–140 kg) remained in the same general area (<90 km from tagging) for up to 5 d during the peak of the spawning season (April) off Baja California (Carey and Robison 1981). More extensive movement occurred for a 70 kg swordfish tracked for 2.5 d in November in the vicinity of Cape Hatteras, North Carolina. This fish traveled 240 km in 67 h, heading from cold continental shelf waters off Cape Hatteras to warmer Sargasso Sea waters. The combination of this information on net random movement of swordfish with our observed histological evidence for recent or imminent spawning suggests that spawning occurs in our sampling area. Additionally, Grall et al. (1983) found major concentrations of swordfish larvae and juveniles in the western Atlantic in the waters near the Lesser Antilles, in the Yucatan Straits, and in the Florida Straits, implying the presence of a large spawning population in these areas.

Changes in sex ratios as swordfish increase in size apparently result from differences in growth between the sexes and possibly from seasonal differences in their distribution. Swordfish larger than ~230 cm are female because males have shorter life spans and slower growth rates (Berkeley and Houde 1984, Wilson 1984). The dominance of males in our summer collections may be explained by seasonal differences in the distribution of the sexes. Guitart-Manday (1964) found a similar preponderance of males (72%) in samples from the mainly summertime commercial fishery off Cuba. Beckett (1974) reported that few males were taken in the northern swordfish fisheries in waters <18°C, whereas in more tropical latitudes, males account for 67–100% of the catch. Off southeast Florida, surface-water temperatures remain >18°C throughout the year, ranging from ~22°C in February to 29°C in August (Atkinson et al. 1983). Our observed seasonal changes in sex ratios of swordfish collected off southeast Florida imply that whereas some males and females are year-round inhabitants of these waters, more females than males move north during the summer, which results in a dichotomous distribution that becomes more acute the farther north the fish migrate. At the northern extent of the range in the western North Atlantic, off New England and the Canadian maritimes, most, if not all, fish captured are females (Lee 1942, Tibbo et al. 1961).

Our estimates of batch fecundity (1.4–4.2 million ova) are comparable to the estimate of Yabe et al. (1959) and to estimates for smaller swordfish by Uchiyama and Shomura (1974). Our estimates are somewhat less than those made for larger fish collected by the latter authors. Yabe et al. (1959) estimated the fecundity of a swordfish 186 cm TRNKL (276 cm LJFL from Table 1) to be 3–4 million ova (1.2–1.6 mm in diameter). Uchiyama and Shomura (1974) estimated the fecundity of an 80 kg swordfish (185 cm LJFL from Table 1) to be 3.0 million ova, which closely agrees with our determinations. However, they estimated that a 200 kg swordfish (244 cm LJFL from Table 1) would have a fecundity of ~6 million ova, which is more than our estimates for swordfish over 200 kg.

Our estimates of fecundity and maturity schedules can be used in analyzing the effect of fishing on the spawning-stock biomass or spawning potential of swordfish in the U.S. South Atlantic (e.g., spawning-stock biomass per recruit analysis, Gabriel et al. 1989). Recent assessments of the status of swordfish in the Atlantic have utilized several techniques, including dynamic pool models ("yield per recruit"), to determine the effects that fishing and age at entry to the fishery have on yield (ICCAT 1991). Our quantitative estimates of the female maturation process and fecundity can be used in further analyzing the effect of fishing on the abundance of mature swordfish (and by implication the production of new recruits).

Acknowledgments

Credit for collecting the samples and data for this research is given to E. Houde, S. Berkeley, E. Irby, J. Jolley, and D. Nickerson. Data collected for this study were funded in part by a grant/cooperative agreement from the National Oceanic and Atmospheric Administration through the National Sea Grant College, Grant NA80AA-D-00038. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. We thank L. French, J. Leiby, M. Myers, and anonymous reviewers for their editorial assistance.

Citations

Arata, G.F. Jr.
1954 A contribution to the life history of the swordfish, *Xiphias gladius* Linnaeus, from the South Atlantic coast of the United States and the Gulf of Mexico. Bull. Mar. Sci. Gulf Caribb. 4:183–243.

Atkinson, L.P., T.N. Lee, J.O. Blanton, and W.S. Chandler
1983 Climatology of the southeastern United States Continental Shelf waters. J. Geophys. Res. 88:4705–4718.

Beckett, J.S.
1974 Biology of swordfish, *Xiphias gladius* L., in the Northwest Atlantic Ocean. *In* Shomura, R.S., and F. Williams (eds.), Proc., Int. billfish symp.; Part 2, Review and contributed papers, p. 105–106. NOAA Tech. Rep. NMFS SSRF 675.

Berkeley, S.A., and E.D. Houde
1980 Swordfish dynamics in the Straits of Florida. Int. Counc. Explor. Sea CM 1980/H:59 Pelagic Fish Committee, 11 p.
1984 Age determination of broadbill swordfish, *Xiphias gladius*, from the Straits of Florida, using anal fin spine sections. *In* Prince, E.D., and L.M. Pulos (eds.), Proc., International workshop on age determination of oceanic pelagic fishes: Tunas, billfishes, and sharks, p. 137–143. NOAA Tech Rep. NMFS 8.

Berkeley, S.A., and E.W. Irby
1982 Analysis of catch, effort and landing data in the swordfish longline fishery of the Florida Straits. Int. Counc. Explor. Sea CM 1982/H:53, 12 p.

Brown-Peterson, N., P. Thomas, and C.R. Arnold
1988 Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in South Texas. Fish. Bull., U.S. 86:373–388.

Carey, F.G., and B.H. Robison
1981 Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fish. Bull., U.S. 79:277–292.

DeMartini, E.E., and R.K. Fountain
1981 Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: Attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547–555.

DeMetrio, G., P. Megalofonou, S. Tselas, and N. Tsimedides
1989 Fishery and biology of the swordfish *Xiphias gladius* L., 1758 in Greek waters. *In* Savini, M., and J.F. Caddy (eds.), Report of the second technical consultation on stock assessment in the eastern Mediterranean, p. 135–145. FAO Fish. Rep. 412.

Fitzhugh, G.R., T.G. Snider III, and B.A. Thompson
1988 Measurement of ovarian development in red drum (*Sciaenops ocellatus*) from offshore stocks. Contrib. Mar. Sci. (Suppl.) 30:79–83.

Gabriel, W.L., M.P. Sizenmore, and W.J. Overholtz
1989 Analysis of spawning stock biomass per recruit: An example for Georges Bank haddock. N. Am. J. Fish. Manage. 9:383–391.

Grall, C., D.P. DeSylva, and E.D. Houde
1983 Distribution, relative abundance, and seasonality of swordfish larvae. Trans. Am. Fish. Soc. 112:235–246.

Grier, H.J.
1981 Cellular organization of the testis and spermatogenesis in fishes. Am. Zool. 21:345–357.

Guitart-Manday, D.
1964 Biología pesquera del emperador o pez de espada, *Xiphias gladius* Linnaeus (Teleostomi: Xiphiidae) en las aguas de Cuba. Poeyana Inst. Biol. (Habana), Ser. B. 1, 37 p. [transl. by Foreign Language Div., Canada].

Humason, G.L.
1972 Animal tissue techniques. W.H. Freeman, San Francisco, 641 p.

Hunter, J.R., and B.J. Macewicz
1985 Measurement of spawning frequency in multiple spawning fishes. *In* Lasker, R. (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, p. 79–94. NOAA Tech. Rep. NMFS 36.

ICCAT (International Commission for the Conservation of Atlantic Tunas)
1991 Reference paper on 1991 swordfish stock assessments by SCRS swordfish assessment group. SCRS/91/16, Int. Comm. Conserv. Atl. Tuna, Madrid, 19 p.

Kume, S., and J. Joseph
1969 Size composition and sexual maturity of billfish caught by the Japanese longline fishery in the Pacific Ocean east of 130°W. Bull. Far Seas Fish. Res. Lab. (Shimizu) 2:115-162 [in Engl., Japanese summ.].

Lee, R.E.
1942 The occurrence of female swordfish in southern New England waters, with a description of their reproductive condition. Copeia 2:117–119.

Markle, G.E.
1974 Distribution of larval swordfish in the Northwest Atlantic Ocean. *In* Shomura, R.S., and F. Williams (eds.), Proc., Int. billfish symp.; Part 2, Review and contributed papers, p. 252–260. NOAA Tech. Rep. NMFS SSRF 675.

Murphy, M.D., and R.G. Taylor
1990 Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. Fish. Bull., U.S. 88:531–542.

Nakamura, I.
1985 Billfishes of the world. FAO Fish. Synop. 125(5), 58 p.

Ovchinnikov, V.V.
1970 Mech-ryba i parusnikovye (Atlanticheskii okean. Ekologia i funktsional naya morfologiya). (Swordfish and billfishes of the Atlantic Ocean. Ecology and functional morphology.) Nauch-Issled. Inst. Ryb. Knoz. Okeanogr., Kaliningrad, 106 p. [Transl. by Israel Prog. Sci. Transl., 77 p.; avail. NTIS, Springfield, VA, TT71-50011.]

Palko, B.J., G.L. Beardsley, and W.J. Richards
1981 Synopsis of the biology of the swordfish, *Xiphias gladius* Linnaeus. NOAA Tech. Rep. NMFS Circ. 441, 21 p.

Rohlf, F.J., and R.R. Sokal
1981 Statistical tables, 2d ed. W.H. Freeman, NY, 219 p.

Saila, S.B., C.W. Reckseik, and M.H. Prager
1988 Basic fishery science programs, a compendium of microcomputer programs and manual of operation. Elsevier, NY, 230 p.

SAS
1982 SAS user's guide: Basics, 1982 ed. SAS Inst., Inc., Cary NC, 923 p.

Sokal, R.R., and F.J. Rohlf
1981 Biometry, 2d ed. W.H. Freeman, NY, 859 p.

Takita, T., T. Iwamoto, S. Kai, and I. Sogabe
1983 Maturation and spawning of the dragonet, *Callionymus enneactis*, in an aquarium. Jpn. J. Ichthyol. 30(3):221–226.

Taning, A.V.
1955 On the breeding areas of the swordfish (*Xiphias*). Pap. Mar. Biol. Oceanogr. Deep Sea Res. Suppl. to Vol. 3:3248–3251.

Tibbo, S.N., L.R. Day, and W.F. Doucet
1961 The swordfish (*Xiphias gladius* L.), its life-history and economic importance in the northwest Atlantic. Fish. Res. Board Can. Bull. 130:1–47.

Tibbo, S.N., and L.M. Lauzier
1969 Larval swordfish (*Xiphias gladius*) from three localities in the western Atlantic. J. Fish. Res. Board Can. 26: 3248–3251.

Uchiyama, J.H., and R.S. Shomura
1974 Maturation and fecundity of swordfish from Hawaiian waters. *In* Shomura, R.S., and F. Williams (eds.), Proc., Int. billfish symp.; Part 2, Review and contributed papers, p. 142–148. NOAA Tech. Rep. NMFS SSRF 675.

Wallace, R.A., and K. Selman
1981 Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Weber, E.C., and S.R. Goldberg
1986 The sex ratio and gonad indices of swordfish, *Xiphias gladius*, caught off the coast of southern California in 1978. Fish. Bull., U.S. 84:185–186.

Wilson, C.A. III
1984 Age and growth aspects of the life history of billfishes. Ph.D. diss., Univ. South Carolina, Columbia, 180 p.

Yabe, H.S., S. Ueyanagi, S. Kikawa, and H. Watanabe
1959 Studies of the life history of the swordfish, *Xiphias gladius* Linnaeus. Rep. Nankai Reg. Fish. Res. Lab. 10: 107-150 [in Jpn., Engl. summ.; transl. by CEP Multilingual Serv. Div., Dep. Sec. of State, Canada].

The index and/or table of contents has been removed and photographed separately within this volume year.

For roll film users, this information for the current volume year is at the beginning of the microfilm. For a prior year volume, this information is at the end of the microfilm.

For microfiche users, the index and/or contents is contained on a separate fiche.

Statement of Ownership, Management and Circulation

(Required by 39 U.S.C. 3685)

1A. Title of Publication	1B. PUBLICATION NO.	2. Date of Filing
Fishery Bulletin	3 6 6 - 3 7 0	9-16-92
3. Frequency of Issue: Quarterly	3A. No. of Issues Published Annually: 4	3B. Annual Subscription Price: 24.00 domestic; 30.00 foreign

4. Complete Mailing Address of Known Office of Publication *(Street, City, County, State and ZIP+4 Code) (Not printer)*
NMFS Scientific Publications Office
7600 Sand Point Way NE, Seattle, WA 98115-0070

5. Complete Mailing Address of the Headquarters of General Business Offices of the Publisher *(Not printer)*
National Marine Fisheries Service, NOAA/DOC
1335 East-West Highway, Silver Spring, MD 20910

6. Full Names and Complete Mailing Address of Publisher, Editor, and Managing Editor *(This item MUST NOT be blank)*

Publisher *(Name and Complete Mailing Address)*
Willis Hobart, Scientific Publications Office
7600 Sand Point Way NE, Seattle, WA 98115-0070

Editor *(Name and Complete Mailing Address)*
Nancy Peacock, Scientific Publications Office
7600 Sand Point Way NE, Seattle, WA 98115-0070

Managing Editor *(Name and Complete Mailing Address)*
Same as above

7. Owner *(If owned by a corporation, its name and address must be stated and also immediately thereunder the names and addresses of stockholders owning or holding 1 percent or more of total amount of stock. If not owned by a corporation, the names and addresses of the individual owners must be given. If owned by a partnership or other unincorporated firm, its name and address, as well as that of each individual must be given. If the publication is published by a nonprofit organization, its name and address must be stated.) (Item must be completed.)*

Full Name	Complete Mailing Address
U. S. Dept. of Commerce	14th St., NW, Washington, DC 20230

8. Known Bondholders, Mortgagees, and Other Security Holders Owning or Holding 1 Percent or More of Total Amount of Bonds, Mortgages or Other Securities *(If there are none, so state)*

Full Name	Complete Mailing Address
NONE	

9. For Completion by Nonprofit Organizations Authorized To Mail at Special Rates *(DMM Section 424.12 only)*
The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes *(Check one)*

(1) [ ] Has Not Changed During Preceding 12 Months
(2) [ ] Has Changed During Preceding 12 Months
(If changed, publisher must submit explanation of change with this statement.)

10. Extent and Nature of Circulation *(See instructions on reverse side)*	Average No. Copies Each Issue During Preceding 12 Months	Actual No. Copies of Single Issue Published Nearest to Filing Date
A. Total No. Copies *(Net Press Run)*	2074	2080
B. Paid and/or Requested Circulation 1. Sales through dealers and carriers, street vendors and counter sales	handled by U.S. Supt. of Documents, Washington, DC 20240	
2. Mail Subscription *(Paid and/or requested)*	"	"
C. Total Paid and/or Requested Circulation *(Sum of 10B1 and 10B2)*	600	600
D. Free Distribution by Mail, Carrier or Other Means Samples, Complimentary, and Other Free Copies	1455	1457
E. Total Distribution *(Sum of C and D)*	2055	2057
F. Copies Not Distributed 1. Office use, left over, unaccounted, spoiled after printing	19	23
2. Return from News Agents	--	--
G. TOTAL *(Sum of E, F1 and 2--should equal net press run shown in A)*	2074	2080

11. **I certify that the statements made by me above are correct and complete**

Signature and Title of Editor, Publisher, Business Manager, or Owner

PS Form **3526**, January 1991 *(See instructions on reverse)*

Superintendent of Documents **Subscriptions** Order Form

Order Processing Code:
* 5178

☐ **YES,** enter my subscription as follows:

Charge your order. It's Easy! MasterCard VISA

To fax your orders (202) 512–2233

____ subscriptions to **FISHERY BULLETIN (FB)** for $24.00 per year ($30.00 foreign).

The total cost of my order is $_____. Price includes regular domestic postage and handling and is subject to change.

_____
(Company or Personal Name) (Please type or print)

_____
(Additional address/attention line)

_____
(Street address)

_____
(City, State, ZIP Code)

_____
(Daytime phone including area code)

_____
(Purchase Order No.)

May we make your name/address available to other mailers? YES ☐ NO ☐

Please Choose Method of Payment:

☐ Check Payable to the Superintendent of Documents

☐ GPO Deposit Account ☐☐☐☐☐☐☐–☐

☐ VISA or MasterCard Account

☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐

☐☐☐☐ (Credit card expiration date)

Thank you for your order!

_____
(Authorizing Signature) 11/91

Mail To: New Orders, Superintendent of Documents
P.O. Box 371954, Pittsburgh, PA 15250–7954

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

Fishery Bulletin

Guidelines for Contributors

Form of manuscript

The document should be in the following sequence: Title Page, Abstract (not required for Note), Text, Acknowledgments, Citations, Text footnotes, Appendices, Tables, Figure legends, and Figures.

Title page should include authors' full names and mailing addresses and the senior author's telephone and FAX numbers.

Abstract Not to exceed one double-spaced typed page. Should include a sentence or two explaining to the general reader why the research was undertaken and why the results should be viewed as important. Abstract should convey the main point of the paper and outline the results or conclusions. No footnotes or references.

Text A brief introduction should portray the broad significance of the paper. The entire text should be intelligible to readers from different disciplines. All technical terms should be defined, as well as all abbreviations, acronyms, and symbols in text, equations, or formulae. Abbreviate units of measure only when used with numerals or in tables and figures to conserve space. Measurements should be expressed in metric units, with other equivalent units given in parentheses. Follow the *U.S. Government Printing Office Style Manual*, 1984 ed., and the *CBE Style Manual*, 5th ed. Fishery and invertebrate nomenclature should follow the *American Fisheries Society Special Publication 12* (for fishes), *16* (for mollusks), and *17* (for decapod crustaceans).

Text footnotes should be numbered in Arabic numerals and typed on a separate sheet from the text. Footnotes are not used for reference material or personal communications, but rather to explain or define terms in the text and for contribution numbers on the title page.

Informal sources Personal communications, unpublished data, and untitled manuscripts in preparation are noted parenthetically in the text (full name, affiliation, brief address including zip code, and month and year when appropriate).

Acknowledgments Gather all acknowledgments into a brief statement at the end of the text. Give credit only for exceptional contributions and not to those whose contributions are part of their normal duties.

Citations All titled sources should be listed in the Citations section, including unpublished and processed material. In text, cite as Smith and Jones (1977) or (Smith and Jones 1977); if more than one citation, list chronologically (Smith 1936, Jones 1975, Doe In press). All sources cited in the text should be listed alphabetically by the senior authors' surnames under the heading CITATIONS. Abbreviations of periodicals and serials should conform to *Serial Sources for the BIOSIS Data Base*™. Indicate whether sources are in a language other than English. For informal literature, include address of author or publisher. Authors are responsible for the accuracy of all citations.

Tables should supplement, not duplicate, the text. Each table should be numbered and cited consecutively, with headings short but amply descriptive so that the reader need not refer to the text. For values less than one, zeros should precede all decimal points. Indicate units of measure in column headings; do not deviate from the unit of measure within a column. Table footnotes should be noted consecutively in Roman letters across the page from left to right and then down. Since all tables are typeset, they need not be submitted camera-ready.

Figures Photographs and line drawings should be of professional quality—clear and concise—and reducible to 42 picas for full-page width or to 20 picas for a single-column width, and to a maximum 55 picas high. All graphic elements in illustrations must be proportioned to insure legibility when reduced to fit the page format. Line weight and lettering should be sharp and even. Lettering should be upper and lower case, and vertical lettering should be avoided whenever possible (except for vertical, y, axis). Zeros should precede all decimal points for values less than one. Reproductions of line artwork are accepted in the form of high-quality photographic prints from negatives or photomechanical transfer (PMT). Halftones should be sharply focused with good contrast. Micron rules should be inserted on electron micrographs, even when magnification is included in the figure legend. There should be clear distinction between identifying letters (press-on or overlay) and background of photograph. Label each figure in pencil on the back. Send only xerox copies of figures to the Scientific Editor; originals or photographic prints will be requested later when the manuscript is accepted for publication.

Copyright Government publications are in the public domain, i.e., they are not protected by copyright.

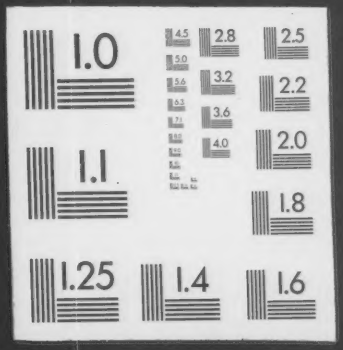
Submission of manuscript

Disks Authors are encouraged to retain manuscripts on word-processing storage media (diskettes, floppy disks) and submit a double-spaced hardcopy run from the storage media. Submit disks as MS-DOS "print" or "nondocument" files (often called "ASCII files"). If a disk cannot be converted to an ASCII file, the author should indicate on the disk the source computer and software language along with the file name. Either 5¼-inch or 3½-inch disks from IBM-compatible or Apple/MacIntosh systems (non-graphics only) can be submitted, double-sided/double-density or high-density, limiting each file to 300 kilobytes. All 8-inch word-processing disks (e.g., Wang or NBI) must be converted onto 5¼- or 3½-inch MS-DOS print disks.

Send original hardcopy and two duplicated copies to:

Dr. Ronald W. Hardy, Scientific Editor
Northwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, WA 98112-2097

Copies of published articles and notes The senior author and his/her organization each receive 50 separates free-of-charge. Additional copies may be purchased in lots of 100.


1.0
1.1
1.25
1.4
1.6
1.8
2.0
2.2
2.5
2.8
3.2
3.6
4.0
4.5
5.0
5.6
6.3